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INTRODUCTION

The Caribbean sea and the thousands of islands and cays composing the Greater and Lesser Antilles are among the most biologically complex areas of the world. Some understanding of this complexity has been achieved in recent years by the application of modern techniques and principles of population genetics, ecology, and island biogeography. To this end, amphibians and reptiles are particularly instructive subjects, but their usefulness in addressing biological problems in the Antilles has not been fully appreciated. Many of the urgent questions remaining about their origins and systematic relationships bear directly on the evolution of the West Indian biota. Among the more valuable data pertinent to such inquiries are the fossil remains of these animals found as owl pellets in limestone caves and sinks. The available West Indian (terrestrial) vertebrate fossil record is no older than late Pleistocene, partly because limestone caves are geologically ephemeral structures, and also because of a general scarcity of nonmarine sediments with the potential of containing older fossils. A few vertebrate fossils of Tertiary age have been recovered from marine sediments, however, including remains of extinct sirenians known from the Eocene(?) to early Miocene of Jamaica, Cuba, Puerto Rico, and Sombrero (see Verona, 1974 for a synopsis), and also shell fragments of a pelomedusid turtle described from the San Sabastian Formation of Puerto Rico (Wood, 1972).

In spite of their recency, the amphibian and reptile fossils from the Antilles often differ from living species taxonomically, morphologically, and distributionally. Herpetofaunal remains are not as well known as are those of birds and mammals, and most amphibian and reptile fossils are from the Greater Antilles. Fossil lizards have received the most attention and have been described from Cuba, Jamaica, Hispaniola, the Bahamas, Cayman Islands, Barbados, and Barbuda by Etheridge (1964a, 1965, 1966a, 1966c), Auffenberg (1959), Hecht (1951), Ray (1964), and Morgan (1977). Extinct tortoises are known from widely scattered localities in the Antilles (Auffenberg, 1967, 1974). Fossils of snakes have been reported from Cuba, the Cayman Islands, and Barbuda (Koopman and Ruibal, 1955; Auffenberg, 1959; Morgan, 1977), but thus far frog fossils have been reported only from Barbuda (Auffenberg, 1959, Lynch, 1966), and the Cayman Islands (Morgan, 1977). Occasionally, amphibian and reptile fossils are also recovered from archaeological sites in the islands.

There has been no thorough treatment of a large fossil herpetofauna and, in general, paleontological research in the West Indies has languished in recent years. Many systematic, zoogeographic, and paleoecological puzzles remain unsolved. For example, on Puerto Rico the only amphibian or reptile fossils known are the isolated remains of the rock iguana, *Cyclura*, the specific identity of which has been questioned since Barbour described it in 1919. Moreover, the cave region of northwest Puerto Rico has been known for years as a rich source of vertebrate fossils, but most of the studies were done over 50 years ago. Wetmore (1920, 1922) described many fossil birds collected by H. E. Anthony, including the extinct barn owl, *Tyto cavatica,* responsible for most of the accumulations of small fossils. A few years later Anthony himself (1925-1926) reviewed the abundance of small mammal fossils. Many of these were bats, but also included were an extinct insectivore, *Nesophontes edithae,* the rodent *Elasmodontomys,* and two species of extinct sloths of the genus *Acratocnis.* More recently, another series of bats and rodents was described by Choate and Birney (1968) from three Puerto Rican caves worked by James W. Bee of the

University of Kansas in 1957. The collection of James Bee also included a number of fossil lizards, but these were not studied. While casually examining this lizard material a few years ago, I found dentaries belonging to the lizard *Leiocephalus,* although the genus presently is not known from the island. While I was pursuing this problem in 1976 and 1977, field parties from the Smithsonian Institution revisited Anthony's localities and excavated new caves. Subsequently, I worked some of these sites in 1978. Thousands of vertebrate bones were recovered from a number of caves. The herpetofaunas from these efforts and those of the James Bee collection are the subject of this paper. The birds and mammals are being studied by other researchers.

The fossil material includes 12 lizards, 4 snakes, 3 frogs, an amphisbaenid and a turtle. There are two new species of *Leiocephalus* and abundant remains of *Cyclura.* The diversity of species exceeds any previously known fossil herpetofauna from the West Indies and as such, invites comparative discussion of the animals past and present.

The first section of the paper describes the physical features of Puerto Rico and the nature of the cave deposits. The majority of the text is devoted to description of the fossils (Systematic Paleontology) with elaboration on the osteology of poorly known species. Because descriptive accounts rely, at least in part, on the availability of adequate comparative material, some species are treated more thoroughly than others.

The last section discusses the fossil assemblages in terms of species composition, bias owing to owl predation, the paleoenvironment, and finally the zoogeographic implications. Studies of this sort lend themselves to wholesale speculation, but it is not my intention to answer, nor even raise all relevant questions. Rather, by exploiting the potential of the Puerto Rican herpetofaunas I have attempted to synthesize pertinent aspects of the fossil record, and in part, focus the paleontological perspective of West Indian amphibians and reptiles.

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cially large contribution to this work.

METHODOLOGY

All fossils were prepared, identified, and catalogued from unsorted material. Fossils were grouped into bones of the same element according to species. Catalogue numbers were assigned to lots of the same element for each species except for holotypes, paratypes, and those shown as figures or specifically referred to in the text. These were assigned individual numbers. Each species account includes material, description, and comments. Material includes all the fossils for that species arranged by abundance in a particular locality and in a skeletal sequence of cranial, appendicular, and vertebral elements. The description is a discussion of osteological features pertinent to the identification of the material. Each description is followed by comments on the morphological implications of the fossils, systematic and taxonomic notes, and the distribution and habits, when known, of the extant animals to which the fossils are referred. Snout-vent length (SVL) estimates were made for the fossil individuals whenever possible. This was done by multiplying the measurements of separate fossil elements against the ratio of body proportions for that skeletal element from known, whole individuals. Ontogeny, allometric growth, and individual variation produce different estimates according to which element is used; for example, dentaries, frontals, or limb bones. Thus, an average, minimum and maximum estimate is given for each bone used in the computation when bones were sufficient in quantity.

Museum acronyms appearing in this paper are as follow:

AMNH   American Museum of Natural History

ASFS   Albert Schwartz, Miami-Dade Community College

FSM   Florida State Museum, The University of Florida

GKP   Gregory Pregill, The University of Kansas

JDL   John Lynch, The University of Nebraska

KU   The University of Kansas Museum of Natural History

KUVP   University of Kansas Vertebrate Paleontology

MCZ   Museum of Comparative Zoology, Harvard University

REE   Richard Etheridge, San Diego State University

RT   Richard Thomas, The University of Puerto Rico

USNM   National Museum of Natural History, Smithsonian Institution

Osteological terminology for lizards follows McDowell and Bogart (1954), Oelrich (1956) and Etheridge (1959); for snakes McDowell (1975) and Pregill (1977); and for frogs Trueb (1973) and Lynch (1971). Fossils were measured with dial calipers read to the nearest 0.1 millimeter. All osteological measurements in the text are expressed in millimeters unless indicated otherwise.

Photographs were made using a Cannon FTb camera mounted on a Wild microscope. First, fossil specimens were placed on pin heads and dusted with ammonium chloride. A pin-mounted specimen then could be inserted into a styrofoam block draped with a black velvet background. Negatives were shot with Kodak Plus-X Pan film (ASA 125). Prints were reproduced on Kodabromide F5 high contrast single weight paper and then arranged together by bone and species.

The number of names applied to island groups of the West Indies often results in confusion as to their geographic limits. In this study, the West Indies include all islands in the archipelago between Florida and northern South America. The Greater Antilles comprise five major islands or island groups and their satellites—The Bahamas, Cuba, Jamaica, Hispaniola (Haiti and Dominican Republic), and Puerto Rico. The Lesser Antilles include all West Indian islands in the archipelago south of Puerto Rico. The name Puerto Rico only refers to the island itself. The term "greater Puerto Rico" or the "Puerto Rican Bank" comprises Puerto Rico and its offshore islets, and the British and U.S. Virgin islands exclusive of St. Croix. A base map of greater Puerto Rico and the islands of the West Indies is presented as Figure 1.

Puerto Rico's herpetofauna was last treated comprehensively by Schmidt (1928), who provided identification keys of the species known up to that time. Mostly I have relied on the check list of Schwartz and Thomas (1975) for much of the taxonomy and distributional data of the West Indian species.

PHYSICAL DESCRIPTION OF PUERTO RICO

Geography.—Centrally located in the West Indies, Puerto Rico lies at the eastern extreme of the Greater Antilles at 18° north latitude approximately half way between the southern tip of Florida to the north and the Caribbean coast of Venezuela to the south (Fig. 1). The island is rectangular with an area of 8,897 km². Topographically it varies from coastal flat lands to peaks of the Cordillera Central which transects the island from east to west. The three principal geographic regions of Puerto Rico are the mountains and foothills of the Cordillera, a discontinuous fringe of more or less flat coastal plain, and the rugged limestone and karst regions oc-

curring primarily in the north central and northwestern part of the island (Fig. 2). The Cordillera Central dominates from Mayagüez on the west coast to Aibonito in the eastern third of the island. Maximum elevation is 1,338 meters at Cerro de Punta in the south central part of the island. The range is met in the east by the Sierra de Luquillo and the Sierra Cayey. The mountains are deeply eroded by streams and valleys to several hundred meters, and slopes of 30° to 40° are common. Rocks are mostly volcanic and include lava, sedimentary rocks derived from basalt, intrusive material and discontinuous beds of limestone. These rocks date from Early Cretaceous to middle Eocene (Monroe, 1976).

The flat, coastal plains slope gently upward from the shore to the foothills. They are characterized by low relief, lagoons, and mangrove swamps and are sporadically peppered by projecting cones of volcanic or intrusive bedrock. The coastal plains grade into alluvial plains of the larger rivers of the island. Except for isolated hills, rocks are Quaternary and consist of sand, clay and gravel from alluvial fans of rivers and as dunes of beach sand.

As in other areas of the Greater Antilles, the limestone and karst regions of Puerto Rico are geomorphic features unique in the Neotropics. The name "karst" is taken from the geologically similar regions of southern Europe. Karst landscape is best developed in a broad limestone belt extending 140 km from the Río Grande Loiza, just south of San Juan, to Aguadilla on the northwest coast. Its widest point is about 22 km near Arecibo. Six formations are recognized in the karst region dating in age from late Oligocene to middle Miocene (Monroe, 1976).

Ecological Life Zones.—According to Ewel and Whitmore (1973) Puerto Rico occupies the Subtropical Latitudinal Region of the Holdridge Life Zone system. Mean annual temperatures at sea level
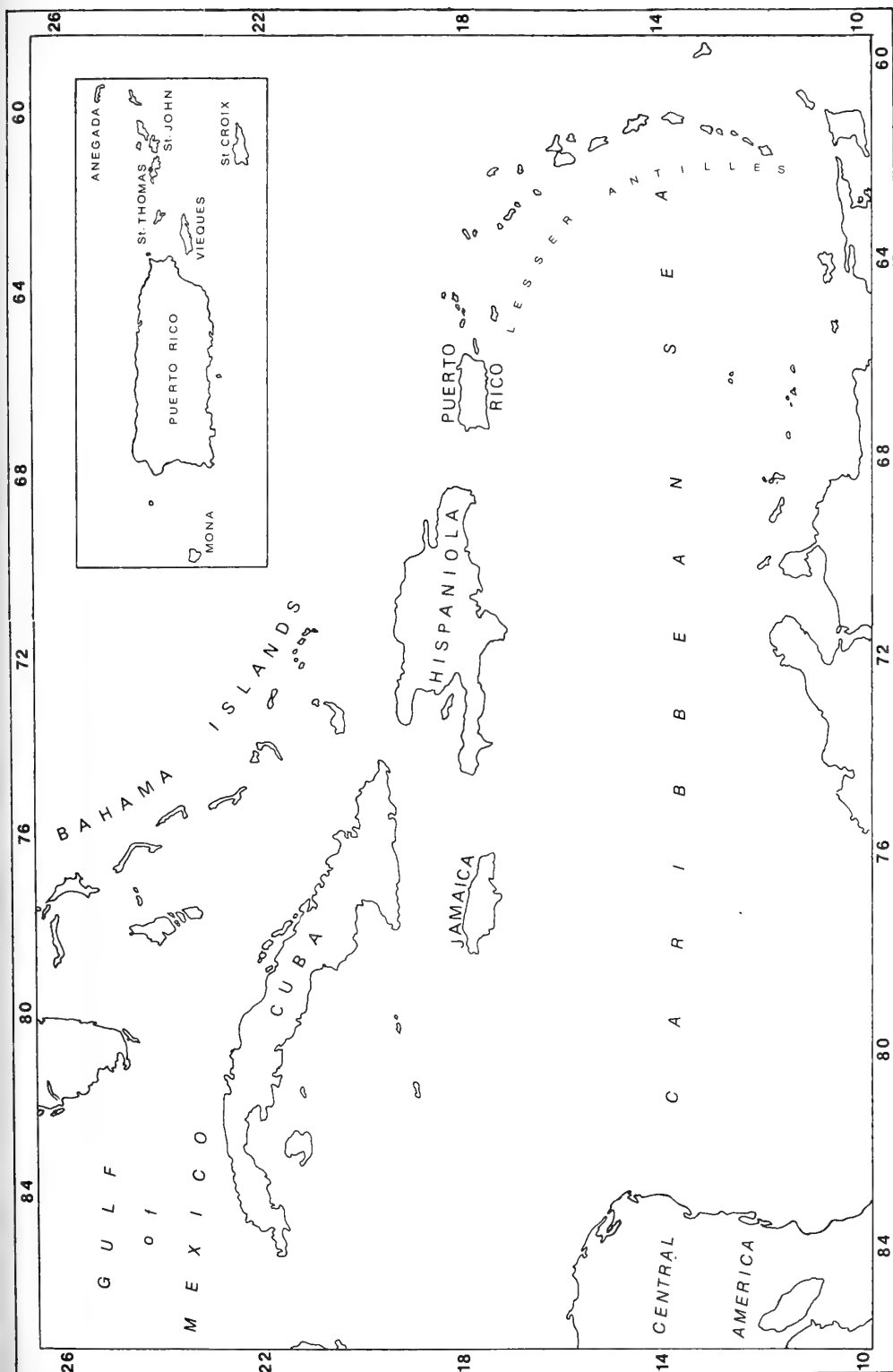
Fig. 1.—Map of the West Indies showing the geographic position of Puerto Rico in relation to the other islands. Inset: Puerto Rico and the U.S. and British Virgin Islands.
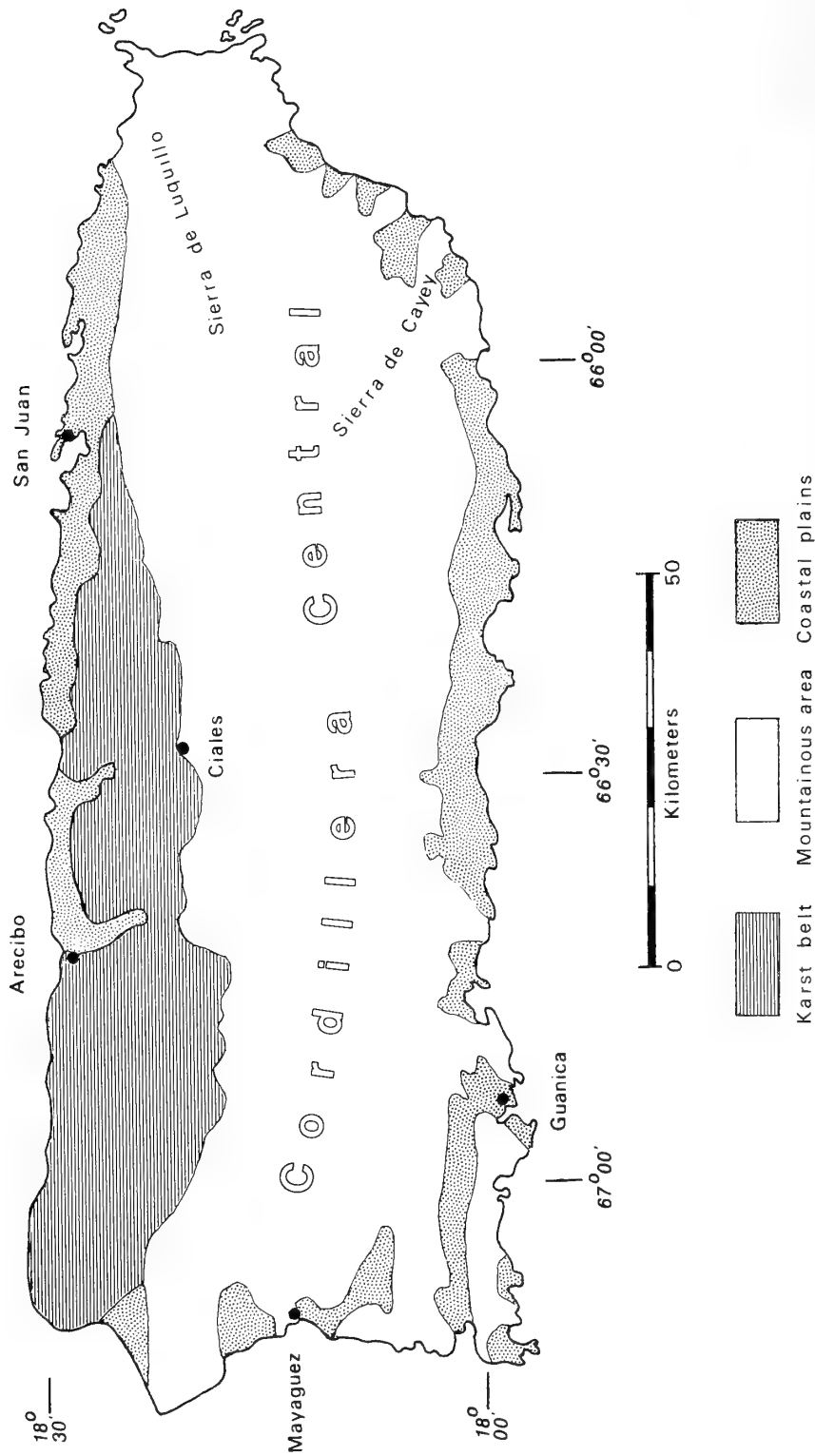
FIG. 2.—Map of Puerto Rico showing the principal physiogeographic regions (after Monroe, 1976).

are less than 24°C, the lower limit of the Tropical Latitudinal Region. This distinction between the geographic tropics—The Tropic of Cancer to the Tropic of Capricorn (23°27′)—reflects differing physiognomies and species composition of sea level forests north or south of 12° to 15° latitude. Six climax forest types occur on Puerto Rico (Fig. 3). These range from Subtropical Dry Forest in the southwestern corner of the island where the mean annual precipitation is between 600 and 1000 mm, to Subtropical Lower Montane Rain Forest in the Luquillo Mountains, which has an annual rainfall of over 4,500 mm (Ewel and Whitmore, 1973).

The more important differences in natural vegetation types are especially impressive considering the short distances over which they occur. However, 60% of the island is covered by Subtropical Moist Forest including the cave regions in the Barahona Valley system from which most of the fossils were obtained (Fig. 4). Subtropical Wet Forest exists at higher elevations of the Cordillera Central and Sierra de Luquillo and accounts for 24% of the island area. Subtropical Rain Forest, Subtropical Lower Montane Wet Forest and Subtropical Lower Montane Rain Forest are restricted practically to the Luquillo mountains and account for less than 3% of the life-zone areas.

Subtropical Moist Forest in the limestone hills presents a continuum of vegetational associations owing to the northeast-southwest orientation of the hills. The hills are humid and moist on the northeasterly facing (windward) slopes and even more so on the southwesterly (leeward) slopes, but they are xeric on top. The average-diameter growth rates of trees on the leeward slopes is nearly twice that of trees on the windward slopes and growth rates at the top of the hills are significantly slower than those on the bottom (Ewel and Whitmore, 1973). Pasture is the predominant land use in the Subtropical Moist Forest,

but sugar cane and coffee occupy large areas; pineapple is grown in the drier portions along the north central and northwest coastal area of the island. The effect of agriculture on the natural habitat undoubtedly has had a significant impact on the distribution of the island's herpetofauna, the ramifications of which are discussed in the section on the paleoenvironment.

The other life zone from which fossils were collected is the Subtropical Dry Forest in the southwest corner of the island near Guánica. The serpentine-derived soil of this area harbors a number of endemic trees and shrubs. Trees are slender, open-crowned and usually less than 12 meters tall (Fig. 5). The forest floor is open because the excessively drained soil supports little herbaceous growth. Most plant species are sclerophyllus and evergreen (Ewel and Whitmore, 1973).

CAVE LOCALITIES AND FOSSIL DEPOSITS

Pleistocene vertebrates from Puerto Rico have been obtained almost entirely from cave deposits. The present section, describing the location and nature of these deposits, particularly those newly discovered, is intended to suffice not only for the fossil herpetofaunas detailed below, but also for future publications by other researchers on the birds and mammals from the same sites. To this end, Storrs L. Olson of the Smithsonian Institution has contributed a substantial portion of the following from his field notes and recollections.

Only a fraction of the hundreds of caves present in the karst regions of Puerto Rico have been explored paleontologically. Caves range in size from small rooms, barely head high, to immense caverns with antechambers and side rooms. Some are entered from ground level (Fig. 6), whereas others are reached only by scaling cliff faces or by climbing down through collapsed
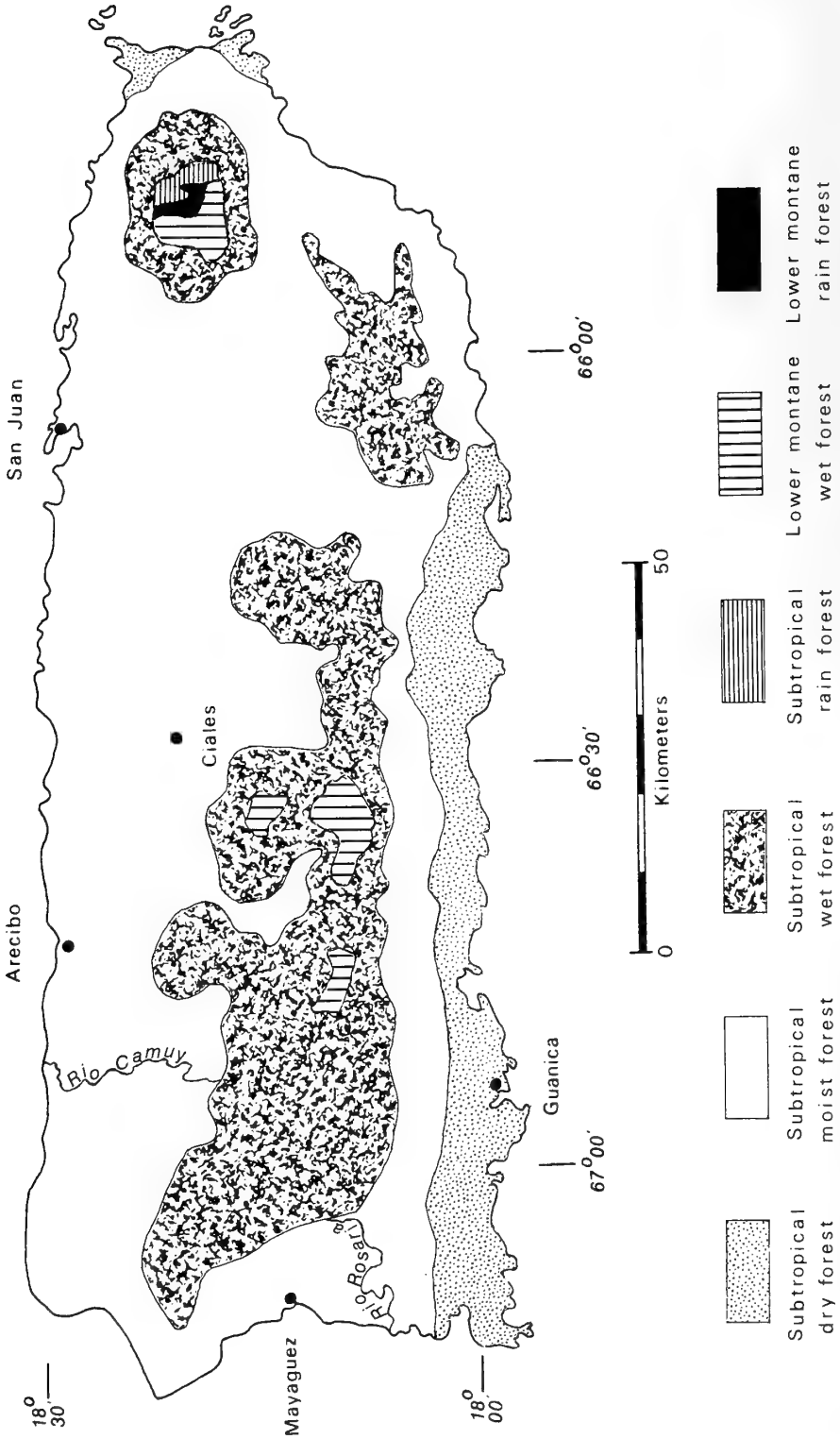
Fig. 3.—Map of Puerto Rico showing the ecological life zones of the island.

Fig. 4.—The Subtropical Moist Forest near the cave region south of Barrio de Barahona, Puerto Rico. Much of this area was cleared for farming in the last century and is now feral pasture and forest.

Fig. 5.—The Subtropical Dry Forest in the vicinity of Guánica Bat Cave of southwest Puerto Rico.

ceilings. The Commonwealth Department of Natural Resources (DNR) maintains a cave inventory and numbering system compiled through the efforts of various speleological groups, but the list is incomplete due to the tremendous number of caves. Reference will be made to the DNR numbers whenever these are known to be applicable.

Purely for descriptive purposes and ease of reference, names are provided for the major fossiliferous caves. These are often whimsical appellations that were applied for convenience in the field, mostly by the Smithsonian expedition. Local names for caves are unreliable for subsequent relocation of sites. Different individuals often have different names for the same cave, the names may

change through time, and there is extensive duplication of names, for example the long list of caves called "Clara" or "Golondrinas."

Most fossils were collected in soil from the floors of the caves in dry, loose, unconsolidated substrate. The bones accumulating as owl pellets are deposited on the floor usually next to a wall, presumably below the owl's roost. When undisturbed, the fossils and soil form a cone-shaped earthen mass resting against the wall. Bones often can be found to depths of several feet, but usually they disappear at the level of the underlying breccia. The cones are excavated and the material is passed through a screen mesh. Typically, cave soil is very fine, and the matrix nearly sifts itself leaving the fossils behind. Vertebrate bone is found in association with a variety of snail shells and claws of land crabs. In some West Indian caves, vertebrate bone, including *Rattus,* is associated with human artifacts in kitchen middens. These deposits are obviously more recent in age than the others (e.g., see Wing, Hoffman and Ray, 1968). Fossils are disassociated and often fragmentary. It is remarkable, however, how many are intact, particularly smaller elements of lizards and frogs. Most fossils are not difficult to prepare save for their small size. The matrix is largely sand and the material can be removed with a sharp probe. Some bones are encrusted with travertine and are permineralized; acid preparation will remove some of this kind of matrix.

The first collections of fossil vertebrates in Puerto Rico were made in 1916 by H. E. Anthony of the American Museum of Natural History. A copy of Anthony's field notes was kindly provided to Storrs Olson by Karl F. Koopman. Three of Anthony's major sites (Cueva Catedral, Cueva Clara and Cueva San Miguel) were located in the center of the island near the town of Morovis (erroneously accented "Morvís" by Wetmore, 1922) and immediately
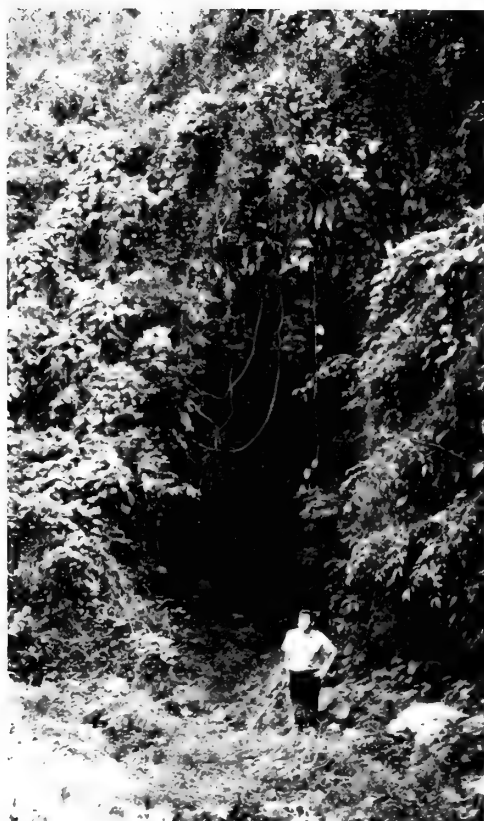
Fig. 6.—A ground level entrance to a cave near Barrio de Barahona, Puerto Rico. Dr. Richard Thomas poses in the foreground.

south of the present village of Barahona. In September 1957, James W. Bee of the University of Kansas Museum of Natural History collected fossils in the same valley system south of Barahona in three caves, all apparently different from any of Anthony's (although one of these was also called "Cueva Clara"). Bee's specimens, including the reptiles and amphibians used in this study and the bats and insectivores described by Choate and Birney (1968), are housed in the University of Kansas Museum of Natural History collection of vertebrate paleontology.

In May 1976, an expedition under the auspices of the Smithsonian Institution collected vertebrate fossils in a variety of localities, but mainly in the above mentioned valley system south of Barahona. Collecting was done by Storrs Olson, Noel Snyder, and Frederick V. Grady, who were assisted in the early stages by Herbert Raffaele, Melvin Ruiz, and John Taapken. Later in 1976 (June 15-22), Snyder, along with Dwight Smith, Carlos Delannoy, José Riveira, Herbert Raffaele, Melvin Ruiz, and Joan Duffield, made additional collections from some of the same caves and also discovered a number of new sites. Subsequently, I visited the island in January, 1978, and traced some of the Smithsonian expeditions and performed additional prospecting, occasionally accompanied by Richard Thomas of the University of Puerto Rico. All of the specimens collected on these expeditions are housed at the National Museum of Natural History, Smithsonian Institution (USNM).

Caves in the Barahona Area.—Probably the most productive area for fossils in Puerto Rico is just north of the center of the island and lies at the southern edge of the karst belt as depicted by Monroe (1976, fig. 2). This is a valley system immediately south of the village of Barahona, 2 km NE of Ciales and 4.5 km NW of Morovis (Ciales Quadrangle, U.S. Geol. Surv. 7.5 minute topo-

graphic map, 1957). The approximate locations of major fossil sites are shown in Fig. 7. From Anthony's (1916, 1918) descriptions and photographs, Noel Snyder was able to locate Cueva San Miguel, but Cueva Catedral and Anthony's Cueva Clara were never identified confidently. Using the maps and descriptions in Bee's field notes, Snyder and Olson were able to correlate Bee's sites with caves they encountered in their explorations. A brief description of the most productive sites is given below.

Blackbone Cave.—In terms of species diversity, this is by far the most productive fossil site yet discovered in Puerto Rico. It was found by the Smithsonian parties who collected there in the spring of 1976. Olson and J. Philip Angle returned to this site in 1977 and removed approximately 135 kg of previously screened (⅛ inch mesh) dirt, which was later passed through finer mesh with the result that many very small vertebrates were recovered that were not represented elsewhere. A sampling bias may have been introduced by this procedure (see Discussion).

Apparently, Blackbone Cave is known locally as "Cueva del Infierno," the name Blackbone having been applied to it by the Smithsonian expedition on account of the exceptional coloration and preservation of the fossils found there. The cave is located 1.2 km due south of Iglesia Ascensión (18° 20′ 57″ N; 66° 26′ 47″ W), as marked on the Ciales Quadrangle topographic map, and comprises an extensive system that runs completely through a ridge of limestone. There are two entrances. The southern entrance is situated in the west side of a small rock shelter concealed in the wall of a large, steep-sided sink. This entrance leads through several dark chambers that ultimately empty into a large, well-lighted room with a collapsed roof. A passageway leads from this room to the second entrance, which is at the edge of a cultivated field. On the northern side of the rubble formed from the rocks of the
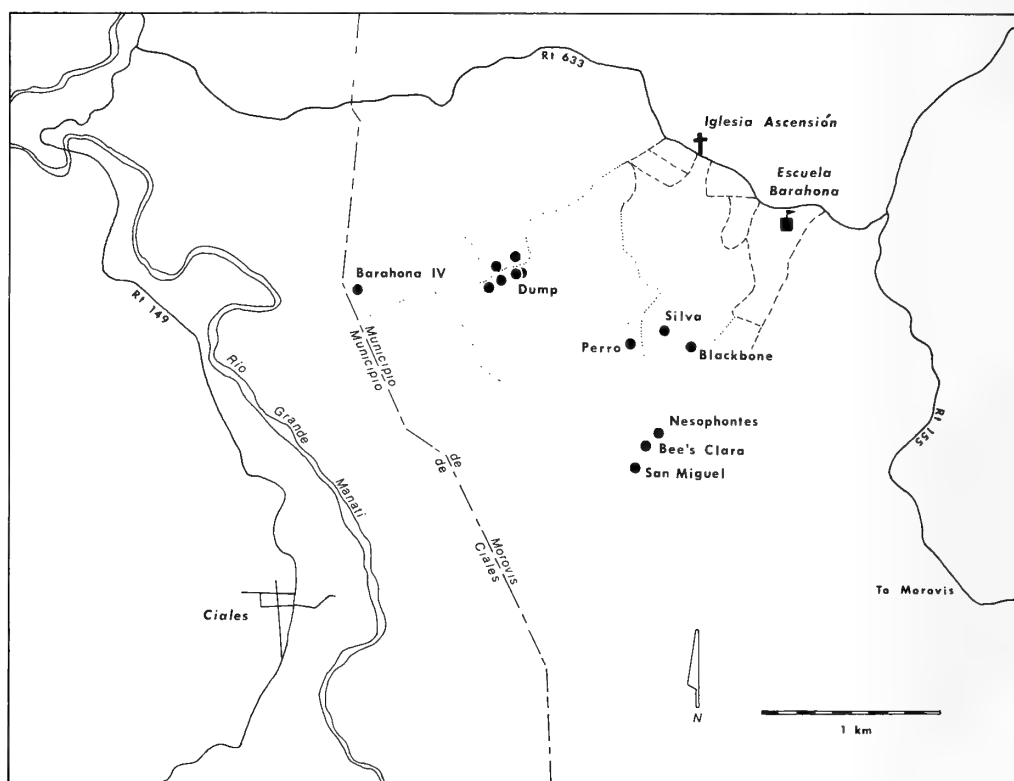
Fig. 7.—Map of the Barahona area, Puerto Rico, with dark circles indicating the approximate locations of the major fossiliferous caves. See text for details.

collapsed roof is a subchamber with a small subsidiary passage at floor level, and another one about 2.5 m off the floor. Beneath the latter was a cone 25 cm deep of loose, fossil-bearing sediment located in a slight pocket in the cave wall. There was no detectable stratification in this cone, which rested on a layer of similar, loose, but nearly barren matrix about 20 cm deep. In turn, this second layer lay on a hard, waxy, red and black clay that was sterile except for a few sloth ribs.

Thousands of bones were obtained here. Their preservation is unusual among West Indian cave deposits in that the bones are black in color, heavily permineralized, hard, dense, unleached and perfectly preserved. In some instances, ossified tendons were preserved on the avian bones. That this deposit was principally the work of owls is attested to by the fossilized pellets that were present, although most bones were found loose and unassociated. This deposit was designated "Blackbone 1" (Fig. 8).

About two to three meters to the right of Blackbone 1, near the mouth of the small, floor-level tunnel, additional bones were found in the sediment on the cave floor. This assemblage was called "Blackbone 2." There were fewer bones here than in Blackbone 1, and their preservation was different also, being lighter in color and usually encrusted with lime.

The collapsed roof of the cave must be of some antiquity, as owls could not have gained access to the large room through either of the long, dark passageways leading to it. Owl roosts in cave

situations, fossil or not, are almost always near an entrance with easy access to the outside.

Nesophontes Cave.—This is another extensive cave system that runs entirely through a hill located about .4 km SSW of Blackbone Cave. Discovered by the Smithsonian expedition, it received its name for the tremendous numbers of bones of the extinct insectivore *Nesophontes* that were recovered there. There are at least three entrances to the cave

and the fossils were found immediately inside the more southerly of these. Here, about 2 m above the cave floor, there was a deposit on one side of the entrance that sloped up for more than a meter to the outside. This deposit consisted of loose, yellowish, dusty soil with an extremely dense concentration of bones. Preservation was entirely different from Blackbone Cave in that the bones were light in weight and buffy colored with a leached appearance. Compared to Black-

Fig. 8.—Storrs Olson (left) and Fred Grady screening fossil matrix inside Blackbone Cave. Photograph by Noel Snyder.

bone Cave, there was a much greater proportion of *Nesophontes* and bats, and correspondingly fewer birds, reptiles, and amphibians.

There was some evidence of former excavation in this cave, as inside the entrance there was a large, rocky pile of what appeared to be tailings. It seems unlikely that this was one of Anthony's or Bee's sites, however, because the cave does not fit any of their descriptions and neither collector obtained *Nesophontes* in such quantities as were found here. The site may have been dug by pot hunters or others looking for indian artifacts. Also, many bat caves were a source of fertilizer for local farmers. The most accessible caves were mined out long ago with the result that other surface contents (including fossils) either have been removed or greatly disturbed.

Bee's Cueva Clara (Fossils collected by Bee from this and his other two sites described below were given University of Kansas locality numbers; for Cueva Clara it is KU-ZCA-02).—Directly across from the south entrance of Nesophontes Cave, across a small valley, is the entrance to another cave with a very high ceiling. Inside, the cave slopes down for a great distance, becoming danker and danker and increasingly populated by bats. As one progresses, there is no small feeling of apprehension. Appropriately, it was dubbed "Horrible Bat Cave" by the Smithsonian expedition. Snyder's party in 1976 found another cave above this one that became "Cave on Top of Horrible Bat Cave." Snyder believes that it is the same as Bee's Cueva Clara (but not the Cueva Clara of Anthony). Bee's field notes describe this cave as being high on a slope and having two entrances. Guano diggers had been there previously and removed most of the soil. Snyder's group recovered a few bones here, preserved in the same way as those from Bee's Cueva Clara.

Cueva San Miguel.—This was one of Anthony's localities (see 1918, Plate 58, Fig. 2), relocated and worked by Noel Snyder's party in 1976. The site is located just south of Bee's Cueva Clara.

Cueva del Perro (KU-ZCA-01).— This was one of Bee's most productive sites and was relocated by the Smithsonian parties in 1976. At this time nothing of interest remained. The cave is situated about .3 km WNW of Blackbone Cave on the western side of a fairly deep valley with a footpath and stream at the bottom. The cave has two entrances. The material Bee removed came from a small, side chamber, with the greatest amount of fossils being found against the wall to a depth of 1.2 m.

Cueva de Silva (KU-ZCA-03).—This is the third of Bee's localities and is located across the valley (east) from Cueva del Perro, on a wall overlooking the sink containing the south entrance to Blackbone Cave. This cave was seen, but not explored by me or the Smithsonian expedition. Bee's notes indicate that the cave soil here was different from that at his other two sites and that he did not collect here extensively.

Barahona IV Cave (18° 21′ 04″ N; 66° 27′ 51″ W).—The Smithsonian party of May 1976 explored a number of caves about 1 km WSW of Barahona in the vicinity of a fairly large refuse dump. These included caves 26, 27, 29, and 30 of the DNR inventory. Little of significance was recovered from any of these. Farther to the west was a more productive site, designated "Barahona IV," and believed to correspond to cave 32 of the DNR inventory. This is an open, airy cave, actually more of a tunnel, with two entrances that run through a hill. Across the valley to the southeast is a similar "through" cave believed to be cave 31 of the DNR inventory. Fossils at Barahona IV were concentrated mostly in dry, reddish soil a few meters in from the north entrance, where the cave becomes constricted and passes into the larger south chamber. Olson, Snyder, and Grady dug and screened here extensively before the more productive Blackbone and Nesophontes Caves were dis-

covered. Bones of extinct rodents were the most frequently encountered fossils, but also present were remains of sloths, birds, and other vertebrates.

There are many lesser caves in the vicinity of Barahona, in some of which the Smithsonian expeditions and myself found usually insignificant samples of fossil bones ("High Cave," "Nancy Robles Cave," "Dwight's Living Heart Sacrifice Cave," "My Cave," "Condor Cave," etc.). These have not been mapped in Fig. 7.

OTHER FOSSIL SITES

Cueva Arcilla.—This is cave 39 of the DNR inventory, located east of Morovis near a small road leading off of Route 159 just beyond the 3.8 km marker. The cave is in a wall at the edge of a banana patch and immediately below a house. It is high and relatively open, sloping up and back for about 18 m. The Smithsonian party of May 1976 obtained a few bones in the red clay along one wall, mostly of the extinct rodent *Elasmodontomys*.

Toraño Cave (18° 18' 05" N; 66° 44' 38" W; Utuado Quadrangle).—This was another of Anthony's (1916, 1918) sites located by the Smithsonian expedition, which found only a few fossils there. It is cave 65 on the DNR inventory and is situated in a mogote in pastureland, 5.7 km NW of Utuado near the settlement of Cayuco. The entrance is a very small opening in a hillside, about 18 m above the surrounding pasture. The cave drops off steeply into a sink, necessitating the use of a rope to descend into it. Anthony's material came from dry earth just inside the entrance, whereas the few bones obtained by the Smithsonian party came from a moist pocket farther inside.

Cueva Soto, Río Abajo (18° 20' 13" N; 66° 42' 25" W; Utuado Quadrangle).—This is cave 157 of the DNR inventory, located 7.6 km north of Utuado in the Río Abajo Forest Reserve. The Smithsonian expedition dug in the white and gray powdery sediments at the front of the cave, but obtained only crab claws,

bat bones, and a few fossils of the extinct flightless rail, *Nesotrochis debooyi*.

Río Camuy Cave (18° 19' 23" N; 66° 49' 27" W; Bayaney Quadrangle).—This is one of a series of caves mentioned by Monroe (1976) along the east bank of the Río Camuy in the northwest part of the island, about .3 km SE of the point where the river goes underground off old Route 129. It is cave 60 of the DNR inventory. The cave is an open shelter with an entrance at either end. The Smithsonian expedition found some specimens near the floor surface adjacent to the walls. The bones were relatively recent in appearance and in association with potsherd and other signs of human occupation. Evidently, this was an archaeological site and was the only locality in which the extinct rodent *Isolobodon* was encountered.

Rosario River Cave.—A very few bones were recovered by Snyder's party from a cave at the western end of the island near Mayagüez, at the south end of the Río Rosario.

Guánica Bat Cave (17° 57' 40" N; 66° 50' 53" W; Punta Verraco Quadrangle).—Located .75 km north of Playa de Tamarindo, this is the only significant site discovered outside of the Barahona area. It differs in being situated in the dry coastal scrub of the southwestern part of the island. The cave, hidden in particularly dense thorn scrub, is entered through a collapsed ceiling that opens into a large, horseshoe-shaped cavern, 25 m high in some places. A number of fossils were collected from a pocket along the east wall in soft, powdery, reddish-brown earth. The bones appear to be more recent in age than from most other sites and are not heavily mineralized. Specimens were collected by Snyder's group in 1976 and by me in 1978.

Age of the Deposits.—One of the major problems in West Indian paleontology is dating fossiliferous cave material. Precise ages of deposition are poorly known. Stratigraphic sequences in a given cave may be present, for ex-

ample a surface layer of 20 cm may be lighter in color than a 20 cm layer below it, but correlation of layers from different caves is meaningless. Hence, fossils have usually been assigned ages such as latest Pleistocene, pre- or post-Columbian, or SubRecent. In some deposits a surface layer of several inches may contain remains of post-Columbian exotics like *Rattus, Mus,* and *Herpestes.* Deeper layers may be characterized by color or "index fossils" peculiar to the cave; one may discuss the lizard layer, *Rattus* layer, *Nesophontes* layer and so forth. However, I think that this assessment is often artifactual because some collectors in the past removed bones selectively.

Hitherto, there have been no attempts made to obtain dates radiometrically or by other sophisticated modern techniques. Difficulties do arise from the lack of appropriate material for dating. Shells of land snails collected from the more productive deposits sampled by the Smithsonian expeditions were submitted by Olson for C^{14} dating to the Smithsonian Radiation Biology Laboratory, where they were analyzed by Dr. Robert Stuckenrath. Snail shells present a special problem in that the carbon used in analysis comes from calcium carbonate of the shells, which may be contaminated by carbonate from extrinsic sources, especially in a limestone environment.

As detailed in the Discussion, there is faunal evidence that the cave deposits from the Barahona area are not all contemporaneous, and if one had to choose a particular deposit that seems unquestionably older than the others it would be Blackbone 1. The other sites are more similar to one another faunally as is the preservation of the fossils, which is not markedly different from that seen in other West Indian deposits. Of two samples of snail shells from Nesophontes Cave, one gave a C^{14} date of 28,300 ± 530 years B.P., whereas the other yielded a date greater than 43,000 years B.P., beyond the effective range of C^{14} dating.

Note that these dates are not consistent with each other. Snail shells from Cueva San Miguel gave a C^{14} date of 35,000 ± 850 years B.P. These all seem widely off the mark and it should be remembered that the bones from the deposits in these two caves appear to be leached.

Three samples of snail shells from Blackbone 1 yielded more believable results. Two samples from the upper 20 cm of the deposit gave dates of 17,030 ± 160 years B.P. and 18,690 years B.P., respectively. One sample from the second 20 cm layer gave a C^{14} date of 21,400 ± 330 years B.P. These dates at least have some stratigraphic consistency, and it is possible that because of the unique preservation of the fossils at this site, the carbonate in the snail shells had not been contaminated. A date of 17 to 20 thousand years before present would mean that the Blackbone 1 deposits were formed during the Wisconsin glaciation when climates and habitats were altered in the West Indies, such that conditions were generally drier. This, too, accords well with the fauna found in the Blackbone 1 deposits (see Discussion).

Tooth fragments consisting mainly of enamel of the rodent *Elasmodontomys* from Barahona IV Cave yielded a C^{14} date of 13,080 ± 335 years B.P. Probably this cannot be relied upon very confidently, however, as it has been determined that enamel, dentine, and cementum from the same tooth can each give different C^{14} dates.

Amino acid racemization analysis can provide useful information on relative ages, but samples of bone and snail shells from the above sites, submitted by Olson to Dr. Ed Hare of the Carnegie Institution of Washington, were too old to be within the effective resolution of the technique.

In summary, the fossil deposits from Puerto Rico indicate that there can be considerable variation in age of deposition and that these deposits may be considerably older than many such deposits

are thought to be. As a tentative working base, the Blackbone 1 fossils are probably about 20,000 years old, whereas the other Puerto Rican deposits are younger.

SYSTEMATIC PALEONTOLOGY

Amphibia

Anura

Leptodactylidae

Two genera of Leptodactylid frogs occur on Puerto Rico—*Leptodactylus* with one species *(L. albilabris)* and *Eleutherodactylus* with 16 species. Both genera are represented by fossils of cranial and post-cranial elements. The diagnostic features of each genus are provided by Lynch (1971) and Heyer (1969b), and fossils of the two are easily distinguishable in this sample. The bones referred to *L. albilabris* are so attributed on the basis of their similarity to the same elements in modern individuals, and the fact that *L. albilabris* is the only representative of the genus on the island. Because osteological descriptions are facilitated by comparison, *L. albilabris* is described with occasional reference to *Eleutherodactylus coqui*, a frog nearly comparable in size.

Leptodactylus albilabris Günther

Material.—Blackbone 1: otoccipitals (4—USNM 259011); sphenethmoids (5 —USNM 259012); maxillae (4 right, 5 left—USNM 259017); mandibles (9 right, 5 left—USNM 259018); scapulae (6 right, 7 left—USNM 259019); ilia (24 right, 19 left—USNM 259013-14); atlases (4 + 1 fragment—USNM 259016); presacral vertebrae (66—USNM 259016).

Blackbone 2: otoccipitals (1—USNM 259020); mandibles (1 partial left— USNM 259021); ilia (2 right, 2 left— USNM 259022); urostyles (2—USNM 259022).

Nesophontes Cave: ilia (5 right, 9 left—USNM 259025).

Barahona IV: scapulae (1 left—

USNM 259024); ilia (1 left—USNM 259023).

San Miguel Cave: pelvic girdle (1 complete—USNM 259026).

Description.—Otoccipital: the four otoccipitals from Blackbone 1 are complete; the specimen from Blackbone 2 is a left half. In this species the exoccipitals and cristae prooticae are narrow, whereas in Puerto Rican *Eleutherodactylus* they are proportionately twice as wide. The occipital condyles are elliptical and widely spaced. In three of the five fossils, a T-shaped parasphenoid is fused to the ventral surface of the prootic. The exoccipital crests are robust and best developed in the larger specimens. The measurements of the four complete otoccipitals at their widest points, across the tips of the cristae prooticae, are 11.6, 15.2, 15.7, 15.8.

Sphenethmoid: five fossil sphenethmoids range in size from 5.2 to 7.0 ($\bar{x} = 6.4$) measured midsagitally. The posterodorsal edge of the sphenethmoid is deeply emarginate with a small posterior projection at the center of the edge. The bone is a hollow box, smooth and flat on the top and bottom. The sides are flared anterolaterally to the level of the palatine articulation. The anterior end tapers abruptly to a blunt point. A bony septumnasi divides the sphenethmoid anteromedially. Each nasal cavity is partially divided by a medially curving septum that arises from the ventral floor. This septum is absent in Puerto Rican *Eleutherodactylus*.

Maxilla: none of the fossil maxillae is complete, however, each bears teeth which distinguish it from the maxilla of Puerto Rican *Eleutherodactylus*. The teeth of *L. albilabris* are larger and more widely spaced. Also, the premaxillary process of the maxilla is expanded dorsally as a thickening of the pars facialis and bears a short peg in contact with the lateral side of the premaxillary bone. In *Eleutherodactylus coqui* the anterior end of the maxilla is simply rounded.

Mandible: 14 mandibles, most of

them missing the symphyseal end, are referred to this species on the basis of a conspicuous coronoid-like process just anterior to the articular surface on the back of the bone. In *Eleutherodactylus* this process is indistinct from the articular surface. The mandibles of both species are smooth and otherwise nearly identical.

Scapula: the scapula of *L. albilabris* is wide and not nearly as constricted in the middle as those of other Puerto Rican frogs. The coracoid articular facet is broadly expanded proximally and raised ventrally. The total length of 14 scapulae ranges between 4.6 and 6.0 ($\bar{x} = 4.9$).

Ilium: numerous ilia are assigned to *L. albilabris* on the basis of the shape of the dorsal prominence. This structure is a large, semicircular expansion at the proximal end of the dorsal crest (Fig. 9). The crest and prominence are compressed in a vertical plane. A rugose, dorsal protuberance covers the posterior half of the prominence on the lateral surface. The ilial shaft is broken at various places distally on most of the fossils, although when complete the shaft is grooved over most of the length of the medial surface and rounded below the groove. Overall, the shaft is gently recurved. The ventral acetabular expansion is smaller than in *Eleutherodactylus coqui* and the preacetabular zone (*sensu* Lynch, 1971:61) is very narrow.

Vertebrae and vertebral column: *L. albilabris* has eight imbricate presacral vertebrae and all but Presacral VIII bear a distinct, posteriorly directed neural spine (Fig. 10). Neural arches are nearly as long as wide. Transverse processes are wide and expanded on Presacrals II, III and IV, but are narrow and unexpanded on the remaining presacrals. The sacral diapophyses are elliptical in cross section, and dialated distally. The sacral diapophyses are directed caudally from the midline of the vertebral column. The two cotyles that receive the urostyle are

FIG. 9.—Fossil ilia of *Leptodactylus albilabris* (top, USNM 259014); *Eleutherodactylus* sp. (middle, USNM 259035); *Peltophryne lemur* (bottom, USNM 259052). Scale equals 5 mm.

separate from one another, whereas in *E. coqui* the cotyles usually are medially confluent. The smallest of eight sacral vertebrae is 5.0 across the diapophyses and the largest is 8.0 ($\bar{x} = 6.7$).

Comments: Leptodactylus is poorly represented in the West Indies. Schwartz and Thomas (1975) included five species in their checklist, but only two of these occur in the Greater Antilles—*L. dominicensis* (Hispaniola) and *L. albilabris* (Puerto Rican Bank). Three species, *L. fallax, L. insularum* and *L. wagneri* range erratically throughout the Lesser Antilles. The relationships of Antillean *Leptodactylus* with other members of the genus is unclear. Heyer (1969a, 1970) placed *L. fallax* in the *pentadactylus* group, *L. insularum* in the *ocellatus*

group and *L. wagneri* in the *melanonotus* group. Heyer referred to the two Greater Antillean forms as *L. mystaceus*, thereby implying conspecificity of *L. albilabris* with *L. dominicensis*, but he did not discuss the reasons for his decision. On Puerto Rico and the Virgin Islands, *L. albilabris* is ubiquitous, occurring anywhere suitable moisture exists.

A minimum of 33 individuals is represented by fossils and 24 of these are from Blackbone 1 alone. The most curious feature of the fossil frogs is their large size. Adults may have reached sizes up to 50% larger than any individual known today. The mean and range of estimated snout-vent lengths of the fossil individuals, based on five different skeletal elements, are as follow: otoccipital width 67.3 (53.5-73.0); sphenethmoid length 74.9 (61.0-82.0), sacral vertebra width 45.2 (34.0-58.5), acetabular diameter 57.0 (38.0-79.0), scapular length 56.0 (46.0-67.0). Small sample size of some elements and individual variation and allometry undoubtedly influence these estimates. For example, in other anurans, Trueb (1977) concluded that sphenethmoid length is a rather variable character in a population of *Hyla lanciformis*. Nonetheless, at least some of the fossil individuals obtained snout-vent lengths well in excess of modern individuals. Of 50 specimens examined by Schmidt (1928), the largest was 49.0 SVL. One fossil otoccipital came from an individual over 80.0 SVL.

Eleutherodactylus spp.

Material.—Blackbone 1: otoccipitals (6—USNM 259027); sphenethmoids (6 —USNM 259028); maxillae (30—USNM 259030); mandibles (42—USNM 259029); scapulae (8 right, 12 left—USNM 259040); ilia (45 right, 39 left—USNM 259031-6); vertebrae (6 atlases, 204 presacrals, 36 sacrals—USNM 259037-8); urostyles (6—USNM 259039).

Blackbone 2: ilia (1 left—USNM 259042).

San Miguel Cave: vertebrae (1 presacral—USNM 259043).

Description.—The fossils referred to *Eleutherodactylus* are quite similar in general morphology to those of *Leptodactylus*, and the features distinguishing the two are pointed out in the description of the latter. However, a few pertinent points remain. For example, on the average the ilia of *Eleutherodactylus* are much smaller than those of *L. albilabris*. The ilia lack a conspicuous dorsal prominence, but retain a small rounded dorsal protuberance (Fig. 9). The distal ends of the ilial shafts are broken from most of the fossils, but otherwise they are unremarkable. The eight nonimbricate presacral vertebrae lack neural spines (Fig. 10). The diapophyses of the sacral vertebrae are straight and not dilated distally. A transverse ridge is present over the neural arch of the sacral vertebrae, but it does not extend onto the diapophyses as it does in *L. albilabris*. Measurements of some of the *Eleutherodactylus* fossils are listed in Table 1.

Comments.—The remarkable osteological similarity of Puerto Rican *Eleutherodactylus* precludes specific identification of the fossils. Perhaps with large skeletal series of both sexes of all species this would be possible to some degree.

Puerto Rico's 16 species of *Eleutherodactylus* inhabit the island from sea level to the rain forests at higher altitudes. With the exception of the widespread *E. coqui*, most species are localized in distribution. They are mostly small frogs and as adults have a snout-vent length from 30.0 to 35.0. *Eleutherodactylus coqui* reaches a maximum snout-vent length of 60.0 (Thomas, 1965) as does the rain forest stream denizen, *E. karlschmidti*. The snout-vent lengths of the fossil individuals vary considerably. For the following skeletal elements the estimates are: sphenethmoid 47.0 (21.0-60.0), ilia 30.0 (18.0-51.0), otoccipitals 42.0 (28.0-55.0), sacral vertebrae 32.0 (15.0-53.0). It is difficult to interpret
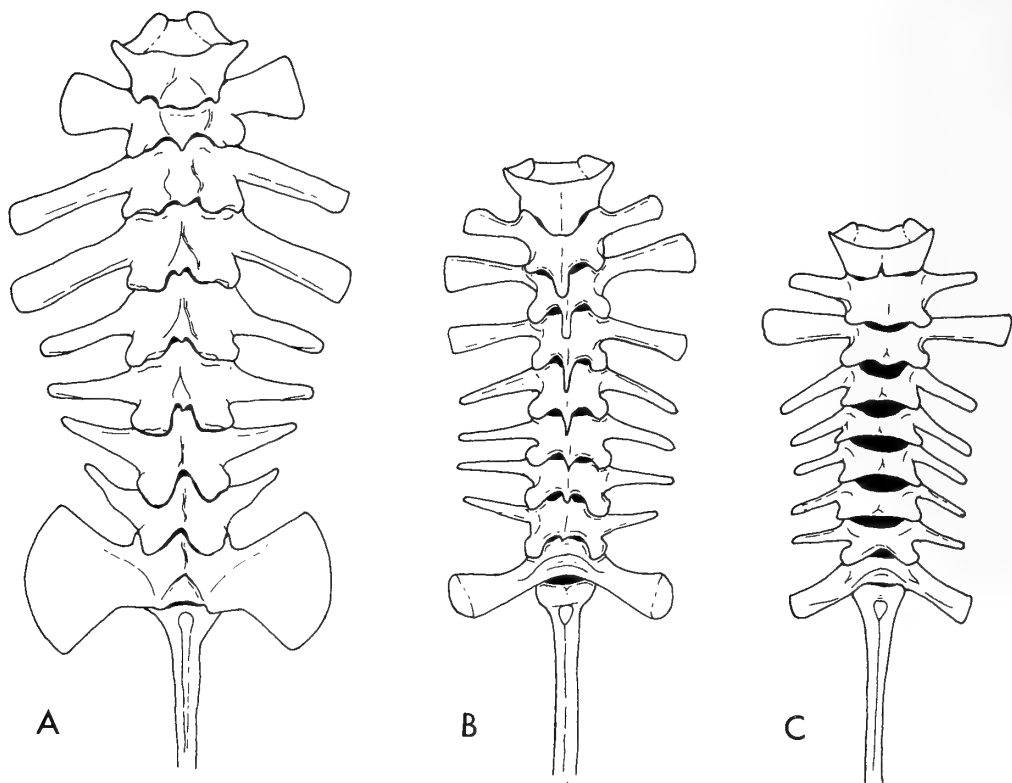
FIG. 10.—The vertebral columns of three Puerto Rican frogs: A. *Peltophryne lemur;* B. *Leptodactylus albilabris;* C. *Eleutherodactylus coqui.*

these values because of the small size of the bones and the error inherent in such estimates. The largest individuals are probably *E. coqui* or *E. portoricensis.* The smaller bones may represent common lowland species such as *E. antillensis* or *E. cochranae.* It is possible that all of the fossils represent one species, although this seems unlikely. In the field, four or five size classes are encountered with nearly equal frequency in winter populations of *E. coqui* (pers. observ.) and these size classes encompass the range of snout-vent length estimates of the fossils. However, larger, adult individuals are more likely to be seen and preyed upon than juveniles and smaller individuals and, hence, a fossil assemblage accumulated through predation would not be likely to contain equal

numbers of juveniles, subadults, and adults.

Bufonidae

Peltophryne lemur Cope

Syn: *Bufo lemur* Cope.
Material.—Blackbone 1: neurocrania (5 right, 6 left—USNM 259044); sphenethmoids (4—USNM 259045); nasals (3 right, 2 left—USNM 259046); squamosals (4 right, 1 left—USNM 259047); maxillae (11 right, 9 left—USNM 259048); mandibles (2 right, 6 left—USNM 259049); scapulae (6 right, 12 left—USNM 259050); suprascapulae (2 right—USNM 259053); ilia (10 right, 21 left—USNM 259051-2); presacral vertebrae (65—USNM 259054-5); sacral vertebrae (9—USNM 259056); urostyles (9—259057).
Blackbone 2: neurocrania (1 right,

TABLE 1.—Selected measurements (mm) of certain fossil elements of *Eleutherodactylus* spp.

	n	$\bar{x}$	Range
Otoccipital width[1]	6	8.7	5.8–11.5
Sphenethmoid:	6		
Midsagittal length		4.0	1.8– 4.5
Anterior width		4.6	2.0– 6.3
Ilia:	76		
Acetabular height[2]		2.5	1.3– 4.2
Sacrum:	28		
Width across diapophyses		4.9	2.3– 8.1

[1] Measured across tips of cristae prooticae.
[2] Measured between tips of dorsal and ventral acetabular expansions.

1 left—USNM 259058); parasphenoids (2—USNM 259060); maxillae (4 right, 1 left—USNM 259059); mandibles (1 right, 3 left—USNM 259061); scapulae (1 left—USNM 259062); coracoids (1 left—USNM 259062); ilia (9 right, 12 left—USNM 259063-4); presacral vertebrae (9—USNM 259066); urostyles (6—USNM 259065).

Guánica Bat Cave: maxillae (1 left —USNM 259067); ilia (1 right, 1 left—USNM 259068); presacral vertebrae (2 —USNM 259070); sacral vertebrae (2—USNM 259070); urostyles (1—USNM 259069).

San Miguel Cave: maxillae (3 left—USNM 259071); presacral vertebrae (2 —USNM 259072); urostyles (1—USNM 259073).

Río Camuy: maxillae (1 right—USNM 259075); ilia (1 right, 1 left—USNM 259076); presacral vertebrae (2 USNM 259076).

Nesophontes Cave: maxilla (1 right —USNM 259074).

Description.—Skull: the skull of *Peltophryne lemur* is well ossified (Fig. 11) and, as a result, many cranial elements are preserved as fossils. The roofing bones are easily distinguishable from those of any other Puerto Rican anuran by their thickness, sculpturing, and prominent canthal, supraorbital and supratympanic crests. Moreover, the maxillary arch bears a pair of "rostral bones" anteriorly which exclude the premaxillae from the tip of the snout. These rostral structures, unique to *P. lemur* and the other eight species of endemic West Indian bufonids, are described in detail elsewhere along with the rest of the skull (Pregill, 1981).

Pectoral girdle: scapulae are abundant as fossils. They are robust structures, proximally bicapitate and approximately the same length as the clavicles. A single coracoid from Blackbone 2 and two suprascapulae from Blackbone 1 are the only other pectoral girdle elements found in the remains. The suprascapula is a more or less rectangular, ossified bone with the cleithrum indistinguishably fused to the posteroventral edge.

Ilia: the ilial shaft of *P. lemur* is a recurved, flattened cylinder bearing a shallow groove on the distal three-fourths of the dorsomedial surface. The ventral acetabular expansion is nearly 90° to the shaft, but the smaller dorsal acetabular expansion is at a less acute angle (Fig. 9). Both the dorsal prominence and dorsal protuberance are well developed. Most of the shafts are broken distally on the fossils. The largest complete ilium is 31.3 measured from the dorsal acetabular expansion to the end of the shaft.

Vertebrae and vertebral column: *Peltophryne lemur* has eight imbricate presacral vertebrae (Fig. 10). The transverse processes are wide on Presacrals II, III and IV, and thin and narrow on Presacrals V, VI, VII and VIII. Neural arches are broad and emarginate on the posterior edge. Low, short neural spines are present on the neural arches of the posterior four or five presacrals. On the anterior presacrals except the atlas, the neural spines terminate as wedge-shaped caps that cover the neural arches. The sacral vertebra has broadly expanded diapophyses and a bicondylic articulation with the urostyle.

Comments.—The abundance of *Peltophryne lemur* as a fossil is striking by contrast to its present scarcity. Schmidt (1928) secured only five specimens for his synopsis, and Grant (1932) reported that only 28 individuals had been col-

lected since the species was first de-
scribed by Cope in 1868. As a result,
nothing is known of its habits. The toad
occurs island-wide at low elevations on
Puerto Rico; although there are records
of this species from Virgin Gorda, British
Virgin Islands, it has not been seen out-
side of Puerto Rico for many years. The
toad is not abundant anywhere in its
range; Richard Thomas informs me, how-
ever, that the animal is probably more
common than currently believed because
of inappropriate collecting methods. Its
presence in five of the fossil localities
suggests that formerly *P. lemur* was more
abundant than it is today. Probably the
animal leads a secretive, semifossorial
existence, a lifestyle which could ac-
count for its rarity in museum collec-
tions. Obviously, it must spend some
time above ground exposed to predation
(e.g. while breeding) in order to account
for the frequency of its occurrence as a
fossil. Schmidt (1928) suggested that
the introduction of *Bufo marinus* to the
island in the early 1920's might account
for the rarity of the species today. *Bufo
marinus* is well established in disturbed
and undisturbed areas over most of the
island and, although it is somewhat
larger, by Schmidt's reckoning *B. ma-
rinus* may be displacing the endemic.
This seems unlikely to me.

The phylogenetic relationships of the
nine endemic species of West Indian

Fig. 11.—The skull of *Peltophryne lemur*
(USNM 27150) shown in dorsal view (top),
ventral view (middle), and lateral view (bot-
tom). Scale equals 5 mm.

Table 2.—Selected measurements (mm) of cer-
tain fossil elements of *Peltophryne lemur*.

	n	$\bar{x}$	Range
Neurocranium:			
Greatest length[1]	9	14.8	13.0–16.8
Maxilla:			
Greatest length	19	22.3	12.2–33.7
Nasal:			
Greatest length	2	16.4	16.4–16.4
Mandible:			
Greatest length	5	20.1	15.7–22.0
Scapula:			
Greatest length	19	9.1	7.1–12.8
Sacrum:			
Width across			
diapophyses	11	13.7	9.7–19.5
Acetabular diameter[2]	44	6.8	4.8– 9.2

[1] Measured along medial border.
[2] Measured from tips of dorsal and ventral
acetabular expansions.

toads were unclear until recently when they were shown to be a natural, monophyletic group, united by a uniquely derived suite of characters that have resulted from dermal co-ossification of the skull, notably the rostral elements at the front of the maxillary arch, and the direct articulation of the zygomatic ramus of the squamosal with the maxillary bone. Consequently, these nine species, *cataulaciceps, empusa, gundlachi, longinasa, peltocephala* and *taladai* (Cuba), *fluviatica, guntheri* (Hispaniola) and *lemur* were given generic recognition for which the name *Peltophryne* (Fitzinger, 1843) was available (Pregill, 1981).

Peltophryne lemur is one of the largest species of Antillean toads. The two largest species (exclusive of *Bufo marinus*) occur on Cuba. *Peltophryne peltocephala* attains a maximum size of 170 snout-vent length and *P. taldai* reaches 147 (Schwartz, 1960; Ruibal 1959). Schwartz (1972) gave a figure of 60 for the maximum size of *P. lemur,* although one female that I measured from the National Museum of Natural History (USNM 27148) has a snout-vent length of 80. The snout-vent length estimates of the fossil individuals range from 43 to 115 and average 80. The estimates are computed from several skeletal elements as follow: neurocrania 67 (59-76), maxillae 76 (43-106), mandibles 83 (64-90), scapulae 88 (73-115), ilia 86 (61-115), sacral vertebrae 74 (52-105). Thus, some members of the fossil populations attained a greater maximum size than any individuals known today. Table 2 lists other measurements of some of the fossils.

Reptilia

Testudines

Emydidae

Chrysemys cf. decussata Gray

Material.—San Miguel Cave: hypoplastron (1 right—USNM 259077).

Description.—The badly worn plastron element referred to this turtle is more or less square and missing most of the lateral margin of the ascending bridge. The bone is 68 long and 64 wide. It came from an individual with an estimated plastron length of 220.

Comments.—Turtles are perhaps the least-studied vertebrates in the West Indies. Their systematic relationships were last treated comprehensively by Barbour and Carr (1940) who recognized six species then assigned to *Pseudemys*. Later, Williams (1956) briefly discussed the West Indian terrapins and placed them in the *ornata* subseries. Five species now are listed as indigenous to the Antilles (Schwartz and Thomas, 1975), but recently Schwartz (1978) suggested that all of them may be conspecific.

Chrysemys decussata stejnegeri occurs throughout Puerto Rico in suitable aquatic habitat. The species also inhabits Cuba, the Cayman Islands, and Hispaniola. The animal is active on land, but its occurrence as a fossil is probably accidental rather than a result of predation.

Sauria

Gekkonidae

Sphaerodactylus sp. indet.

Material.—Blackbone 1: frontals (2 —USNM 259078).

Description.—Two complete frontal bones from Blackbone 1 are the only gekkonid skeletal elements present from the entire fossil assemblage. They are identified by their shape and very small size. The descending laminar processes are fused medially to enclose the olfactory canal as in other gekkos. The two frontals are 2.3 and 2.5 in length, respectively. The supratemporal processes diverge posterolaterally from the parietal border and are 1.8 and 1.9 from tip to tip in each bone. Both specimens are constricted in the middle to a width of 0.5, but expand to 1.1 and 1.2 across their respective anterior borders. The nasal processes are short pegs projecting

craniad from the lateral edges of the anterior border.

Comments.—Currently, five species of *Sphaerodactylus* inhabit Puerto Rico —*S. macrolepis, S. nicholsi, S. klauberi, S. roosevelti,* and S. *gaigae* (Thomas and Schwartz, 1966). Two of these, *S. macrolepis* and *S. klauberi,* are fairly widespread. Commonly, all are collected near underbrush, and by raking leaf litter on forest floors. These lizards are small, ranging in size from 23 to 35 as adults. The snout-vent length of the individuals represented by fossils is approximately 30.

Iguanidae

Anolis

The genus *Anolis* is distinctive osteologically in ways that make identification of fossils to the generic level uncomplicated in most instances. However, at the species level the task is anything but routine. Skeletal differences of closely related species are often subtle and qualitative when they exist at all. Thus, identification requires repeated comparison of skeletal series. Size classes when discrete are a convenient and usually reliable means of reducing the number of potential species to which a given fossil bone could be referred. Accordingly, the many fossils of this lizard are sorted into three groups—bones from lizards with a snout-vent length over 100, those from 60 to 70 and those less than 60, typically between 45 and 55. *Anolis cuvieri* is the only Puerto Rican anole to exceed a snout-vent length of 100. The intermediate size class includes *Anolis cristatellus, Anolis cooki* (*Anolis cristatellus cooki* Grant) and *Anolis gundlachi.* The fossils of this size-group are referred to *A. cristatellus* for reasons pointed out below. Six of Puerto Rico's ten species of *Anolis* are less than 60 as adults and are the most difficult to distinguish osteologically. Certain features distinguish some of these, but most of the material from small anoles is lumped as *Anolis* spp.

Anolis cuvieri Merrem

Material.—Nesophontes Cave: dentaries (10 right, 10 left—USNM 259092-4); articular + surangular (1 right, 7 left—USNM 259095); maxillae (12 right, 10 left—USNM 259096-7); prefrontals (1 left—USNM 259099); frontals (4—USNM 259098); basales (3—USNM 259100); pelves (4 right—USNM 259101); vertebrae (6 dorsal, 1 sacral, 10 caudal—USNM 259102).

Cueva del Perro: dentaries (2 right, 3 left—KUVP 11472); maxillae (4 right, 3 left—KUVP 11473); frontals (1—KUVP 11473); parietals (3—KUVP 11473); basales (2—KUVP 11472); pterygoids (1 left—KUVP 11473); pelves (12 right, 11 left—KUVP 11475); vertebrae (3 dorsal, 2 caudal—KUVP 11475).

Barahona IV: dentaries (2 right, 3 left—USNM 259111); articular + surangular (1 right, 1 left—USNM 259113); maxillae (1 right, 3 left—USNM 259112); prefrontals (2 left—USNM 259115); frontals (2—USNM 259114); basale (1—USNM 259118); quadrates (2 left—USNM 259115); jugals (1 left —USNM 259115); scapulae (3 left—USNM 259116); pelves (1 left—USNM 259117); vertebrae (9 dorsal, 11 caudal —USNM 259119).

San Miguel Cave: dentaries (1 left —USNM 259104); articular + surangular (2 right, 1 left—USNM 259105); maxillae (1 left—USNM 259106); frontals (1 —USNM 259107); parietals (1—USNM 259108); jugals (1 right—USNM 259108); basioccipital (1 fragment—USNM 259109); pelves (2 left—USNM 259110).

Blackbone 1: dentaries (3 right fragments—USNM 259079); articular + surangular (1 right, 1 left—USNM 259080); maxillae (1 right, 1 left—USNM 259081); prefrontals (1 left—USNM 259082); postorbitals (1 right—USNM 259083); jugals (1 left—USNM 259082); pelves (1 right, 3 left—USNM 259084); dorsal vertebrae (22—USNM 259085); caudal vertebrae (6—USNM 259086).

Cueva Clara: dentaries (5 right, 7

left—KUVP 11526); articular + surangular (1 partial left—KUVP 11526); coronoids (1 left—KUVP 11526).

High Cave: dentaries (1 right, 1 left fragment—USNM 259122); quadrates (1 right—USNM 259123); jugals (2 left—USNM 259123); pterygoids (1 partial left—USNM 259124); pubis (1 left—USNM 259124); vertebrae (3 dorsal—USNM 259125).

Blackbone 2: dentaries (1 right fragment—USNM 259087); articular + surangular (1 right fragment—USNM 259087); maxillae (2 right—USNM 259088); pelves (1 right—USNM 259089).

Guánica Bat Cave: mandibles (1 right—USNM 259090); dentaries (2 right, 1 left—USNM 259091).

Cuevo de Silva: dentaries (1 right, 1 left—KUVP 11573); maxillae (1 right KUVP 11573).

Río Camuy: dentaries (2 left—USNM 259120); maxillae (1 left—USNM 259121).

Cueva Toraño: dentaries (1 right—USNM 259126); articular + surangular (1 left—USNM 259126).

Rosario River: dentaries (1 left—USNM 259103).

Robles' Cave: dentaries (1 left fragment—USNM 259126).

Description.—*Anolis cuvieri* is distinguished from all other Puerto Rican anoles by its larger size. Among other West Indian giant anoles, it is the only species lacking a splenial (Etheridge, 1959). Sexual dimorphism is pronounced in *A. cuvieri* and in other giant anoles as well. Rugose ornamentation covers virtually all dorsal roofing bones of adult males, whereas in females these bones are smooth. The parietal of adult males develops a horizontal triangular plate fused to the underlying parietal crests. The base of the triangle abuts the posterior border of the frontal bone. In adult females, the plate is absent and the parietal is simply crested as in other species of *Anolis*.

Dentaries of both sexes are long and tapering, but in males the labial face is scored by irregular folds and grooves (Fig. 12). The posterior teeth of the dentary and maxilla have truncated crowns with weakly developed lateral cusps in adults and juveniles of both sexes. The anterior teeth are simple and pointed. The angular and retroarticular processes are broad and continuous with one another, and extend laterally and posteriorly well beyond the articular surface for the quadrate. A small, hooklike process is present on the lateral side of the articular surface. Measurements of the more abundant fossil elements are listed in Table 3. The basale and frontal are shown in Figures 12 and 14.

Comments.—*Anolis cuvieri* is an arboreal lizard confined to Puerto Rico in widely scattered localities from sea level to 1200 m (Schwartz and Thomas, 1975). Snout-vent length estimates made from the fossils indicate that some individuals from nearly all fossil localities achieved
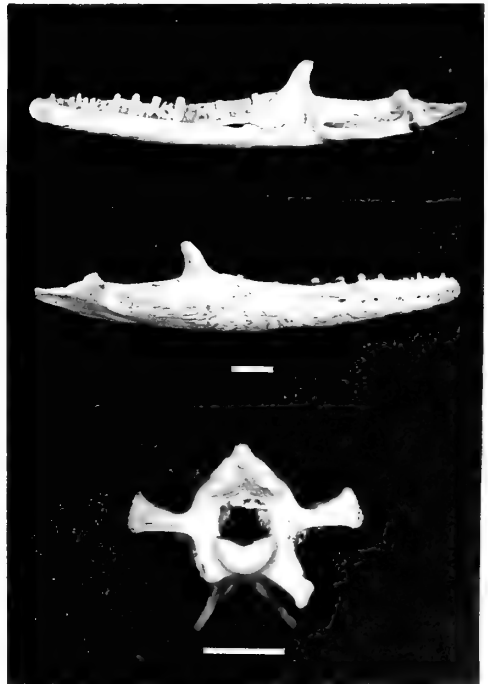

Fig. 12.—Fossils of *Anolis cuvieri:* mandible (top and middle, USNM 259090); basale in occipital view (bottom, USNM 259107). Scale equals 5 mm.

sizes greater than 140—the maximum snout-vent length of Recent individuals. The means and ranges of snout-vent length based on five skeletal elements are, as follow: dentaries 145 (103-175), maxillae 138 (133-161), frontals 135 (127-161), basales 135 (113-165), acetabula 180 (124-212).

Anolis cf. cristatellus
Duméril and Bibron

Material.—Blackbone 1: dentaries (5 right, 3 left—USNM 259127-8); articular + surangular (4 right, 2 left—USNM 259129); maxillae (1 left—USNM 259130); jugals (3 left—USNM 259132); basales (3—USNM 259131); pterygoids (1 right—USNM 259132).

Barahona IV: dentaries (1 right—USNM 259134); articular + surangular (1 right, 1 left—USNM 259134); maxillae (1 left—USNM 259135); frontals (1 fragment—USNM 259135).

San Miguel Cave: mandibles (1 right—USNM 259139); dentaries (3 left—USNM 259138).

Nesophontes Cave: dentaries (2 left—USNM 259136); maxillae (1 right, 1 left—USNM 259137).

TABLE 3.—Selected measurements (mm) of certain fossil elements of *Anolis cuvieri*.

	n	$\bar{x}$	Range
Dentary:			
Tooth row length	26	24.2	17.5–31.9
Number of teeth	26	25.9	22.0–31.0
Articular + surangular:			
Greatest length	9	24.1	20.1–27.7
Length of retro. process	9	7.3	6.6– 9.2
Maxilla:			
Tooth row length	11	22.4	21.5–26.1
Number of teeth	11	22.0	19.0–25.0
Frontal:			
Midsaggital length	7	13.3	12.5–15.9
Posterior width	7	12.7	11.8–15.1
Parietal:			
Greatest length	4	11.8	9.4–13.8
Basale:			
Length[1]	6	8.7	7.9– 9.2
Width[2]	6	14.6	12.3–17.6
Acetabular diameter	25	5.8	4.0– 6.8

[1] Measured from apex of angle formed by pterygoid processes to the lip of the occipital condyle.

[2] Measured across paraoccipital processes.

Cueva del Perro: mandibles (1 right—KUVP 11473); dentaries (1 right, 1 left—KUVP 11473).

Blackbone 2: dentaries (2 right, 1 left—USNM 259133).

Description.—This fossil material belongs to a moderate-sized (60-70) anole, but only the dentaries can be referred to *A. cristatellus* with a high degree of confidence. The dentary of *A. cristatellus* is robust and convex midventrally. In males of this species, the ventrolabial face is sculptured with swollen irregular bumps and excavations which are replaced by horizontal grooves posteriorly (Fig. 13). The dentaries of females are smooth. Teeth are straight, robust, and closely spaced, numbering about 24. The anterior teeth terminate as simple points, whereas those posteriad have short, tricuspid crowns. The transition from simple to tricuspid teeth occurs gradually over three or four teeth between the ninth and seventeenth teeth. Of 19 dentaries referred to this species, the largest, from Nesophontes Cave, has a tooth row 13.0 long and the smallest, also from Nesophontes Cave, is 8.9. They came from individuals with snout-vent lengths of approximately 80 and 55, respectively. The average tooth row length of all fossil dentaries is 10.1—individuals with a snout-vent length of about 62.

Maxillary teeth are like those on the dentary, but the smallest teeth are in the middle of the dental row. The basisphenoids of *A. cristatellus* are distinctive in that the anterior border is curvilinear and has a sharp median indentation. The lateral edges of the pterygoid processes continue caudally as ridges bordering the sphenoccipital tubercles.

Comments.—I was unable to discern any osteological features that would distinguish *A. cristatellus* from *A. gundlachi* other than the dentary sculpturing and shape of the basisphenoid. Adult males of *A. gundlachi* also have a sculptured lower jaw described and figured by Etheridge (1959:123) as a row of from 7 to 10 transverse, semilunar notches on

the ventrolabial surface. This type of sculpturing is found also on *A. pulchellus*. None of the fossil dentaries referred to *A. cristatellus* have this pattern, but about half are intermediate between the *cristatellus* type and the *gundlachi* type. That is, semilunar notches are present as in *A. gundlachi*, but the notches are thrown into irregular folds and grooves as in *A. cristatellus*. The dentary shown in Figure 13 is of this intermediate type, and in fact, the sculpturing on the fossils is in general more robust and extensive than on any recent skeleton that I examined.

One can only speculate as to the significance of the sculpturing on the fossils. *Anolis cristatellus* and *A. gundlachi* are ecomorphic equivalents at low and high altitudes respectively (Rand, 1964; Gorman and Hillman, 1977). The intermediate sculpture pattern on the fossils may be from an ancestral population from which *A. cristatellus* and *A. gundlachi* only recently differentiated. Or possibly, the pattern may occur in a population of one of these species today, but representatives were not present in my sample of modern skeletons.

Anolis cooki (*Anolis cristatellus cooki* Grant) is indistinguishable osteologically from *A. cristatellus*.

Anolis evermanni Stejneger

Material.—Blackbone 1: dentaries (2 left—USNM 259140-1).

Description.—The two dentaries referred to this species are 9.8 and 10.3 along the tooth row and have 24 and 27 teeth or empty alveoli, respectively. They came from individuals with snout-vent lengths between 55 and 60. Features of the dentary which identify this lizard are the elongate, linguilabially compressed shape of the bone and the medial constriction of the dental shelf (Fig. 13). Anteriorly, the shelf is produced into a thickened, convex border. The shelf narrows posteriad gradually to the middle of the tooth row where it dips ventrally. Here the bases of the teeth are flush
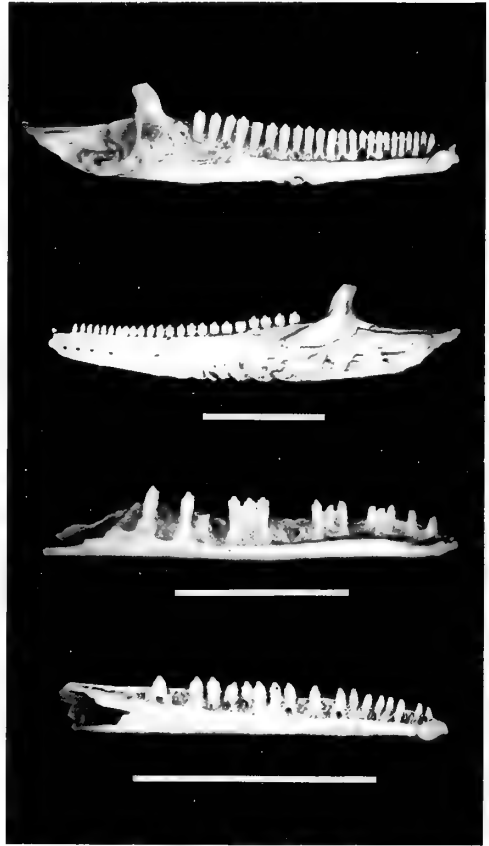
FIG. 13.—Fossil dentaries of 3 species of *Anolis*. From top to bottom: *A. cristatellus* (lingual and labial view, USNM 259128), *A. evermanni* (lingual view, USNM 259140), *A. occultus* (lingual view, USNM 259144). Scale equals 5 mm.

with the lingual edge of the shelf. The dental shelf widens again posteriorly and arches dorsad to the coronoid. In other Puerto Rican anoles the dental shelf is uniform and essentially horizontal. Teeth of *Anolis evermanni* are high and narrow, and closely spaced. They have sharp, tricuspid crowns except for the anteromost eight or ten. These teeth are pointed.

Anolis krugi Peters

Material.—Blackbone 1: frontals (1 —USNM 259142).

Description.—A single frontal bone 6.2 in length belongs to this species. The

frontal of *A. krugi* is unique among Puerto Rican *Anolis* in that the parietal border is convex (Fig. 14). The convex border is received by a corresponding indentation in the frontal border of the parietal. The frontal-parietal suture is straight in other Puerto Rican anoles.

Anolis occultus Williams and Rivero

Material.—Blackbone 1: dentaries (7 right, 5 left, 9 fragments—USNM 259143-4); maxillae (1 right, 3 left—USNM 259146); frontals (2—USNM 259145).

Description.—The diminutive size of this lizard is one of its most obvious characteristics. The very small dentaries are long and narrow (Fig. 13); the 12 fossils have an average tooth-row length of 5.6 and range from 3.6 to 7.2. The smallest specimen has 16 teeth or empty alveoli and the largest 23. The dental shelf is broad and horizontal throughout its length, with negligible dorsal curvature at the coronoid end, as is the case of other Puerto Rican species of *Anolis*. The lower jaw of juvenile *Anolis stratulus* is similar in size and shape, but the bone of this species is more tubular and the teeth are higher and narrower with better developed tricuspid crowns. Teeth of *Anolis occultus* are small, somewhat constricted at their bases, and inflated in the middle. Most teeth terminate in simple blunt points, although the posterior third of the dental series have a faint suggestion of tricuspid crowns.

Williams et al. (1965) noted the absence of a canthal ridge in this species. This feature is evident on the maxilla by its low, medially arching nasal process. Maxillary teeth are similar to those on the dentary.

The frontal bone of *Anolis occultus* is diagnostic. The bone is nearly as wide as long, has little medial constriction, and the supratemporal processes are reduced (Fig. 14). The average ratio of midsaggital length divided by the narrowest width (the medial constriction) is 1.8 (1.5-2.1) for fossil and recent frontals that I examined. The value is considerably greater in other *Anolis*. For example, in *A. cristatellus* the ratio is 3.4 to 3.8, in *A. gundlachi,* 3.4 to 3.6, in *A. stratulus,* 3.8 to 4.2, in *A. evermanni,* 2.8 to 3.2 and in *A. krugi,* 3.5 to 3.9.

The largest specimen of *A. occultus* reported by Williams et al. (1965) had a snout-vent length of 42. The largest fossil dentary came from an individual estimated at 47. The average was 35.

Anolis spp.

Material.—Blackbone 1: dentaries (13 right, 10 left—USNM 259147); articular + surangular (1 right, 2 left—USNM 259147); coronoids (3 right—USNM 259150); maxillae (20 right, 22 left—USNM 259148-9); premaxillae (4—USNM 259149); frontals (14—USNM 259152); parietals (3—USNM 259153); basales (5—USNM 259151); quadrates (1 right, 2 left—USNM 259150); jugals (1 right, 3 left—USNM 259153); pterygoids (1 right—USNM 259151); scapulae (2 right, 2 left—USNM 259154); pelves (7 right, 6 left—USNM 259154); vertebrae (several hundred—USNM 259155-7).

Comments.—Much of the fossil material of *Anolis* is unidentifiable to species and comes from individuals with snout-vent lengths between 45 and 60. This size class includes *A. pulchellus, A. krugi, A. evermanni, A. stratulus* and *A. poncensis.* For the most part the fossils are fragmentary, and because of ontogenetic and individual variation as well as structural similarity of a given bone from one species to another, an attempt at specific allocation would be irresponsible. *Anolis pulchellus* and *A. stratulus* could be expected in this sample because these two forms presently are common at low elevations on the island (Gorman and Harwood, 1977). No doubt further material of *A. evermanni, A. krugi* and *A. occultus* are among these remains as well. *Anolis evermanni* is found in mesic situations in the interior, higher altitude areas of Puerto Rico. *Anolis occultus* is a canopy

dweller that sleeps on exposed perches, also mostly in the higher reaches of the island. Like *A. cristatellus* and *A. gundlachi, Anolis pulchellus,* and *Anolis krugi*

FIG. 14.—Fossil frontal bones of *Anolis cuvieri* (top, USNM 259107), *A. krugi* (middle, USNM 259142), *A. occultus* (bottom, USNM 259145). All are shown in dorsal view. Scale equals 2 mm.

are ecomorphic equivalents at low and high elevations, respectively.

Cyclura pinguis Barbour

Syn: *Cyclura mattea* Miller; *Cyclura portoricensis* Barbour.

Material.—Blackbone 1: dentaries (1 right in two pieces, 1 left in two pieces —USNM 259158-9); surangular (1 left —USNM 259162); maxillae (2 left— USNM 259160-1); parietals (1—USNM 259163); quadrates (1 left—USNM 259164); scapulae (1 right, 1 partial left —USNM 259163); clavicles (1 right, 1 left—USNM 259165); humeri (1 left— USNM 259166); ulnae (1 complete left, 1 proximal left—USNM 259167); radii (1 right, 1 proximal left—USNM 259168); femora (1 right, 1 left—USNM 259169); fibulae (1 left—USNM 259170); tibiae (2 right, 1 left—USNM 259171); tarsals (4—USNM 259172); metatarsals (5— USNM 259172); phalanges (3—USNM 259172); vertebrae (34—USNM 259173).

Blackbone 2: articular (1 left— USNM 259177); premaxillae (1—USNM 259176); postfrontal + postorbital (1 right—USNM 259178); parietals (1— USNM 259175); basales (1—USNM 259174); jugals (1 left—USNM 259178); clavicles (2—USNM 259179); humeri (1 distal right—USNM 259181); radii (1 right—USNM 259181); metacarpals (2—USNM 259181); ilia (1 right— USNM 259180); femora (1 partial right —USNM 259181); vertebrae (3 dorsal, 1 sacral, 5 caudal—USNM 259182).

San Miguel Cave: pterygoids (2 right—USNM 259184-5); palatines (1 right—USNM 259186); humeri (1 left— USNM 259187); pubis (1 left—USNM 259188); femora (1 proximal left—USNM 259187); tarsals (1 astragalus—USNM 259188); vertebrae (1 dorsal, 3 caudal —USNM 259188).

Cueva Clara: parietals (1—KUVP 11564); ulnae (1 proximal left—KUVP 11564); tibiae (2 proximal right—KUVP 11564); fibulae (2 right—KUVP 11564); vertebrae (3 dorsal, 3 caudal—KUVP 11564).
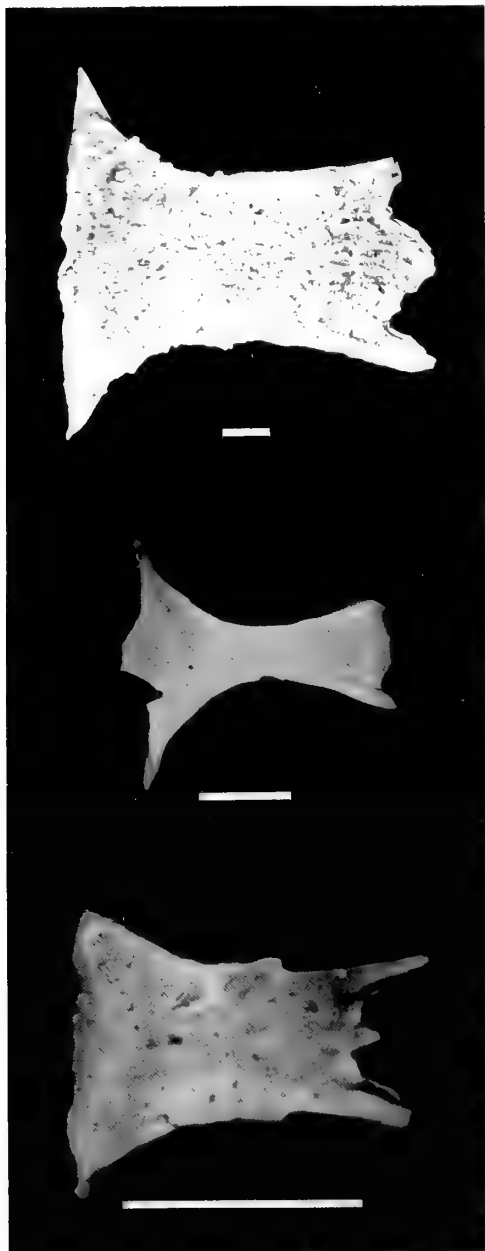
Cueva del Perro: dentaries (1 partial right—KUVP 11472); vertebrae (3 caudal—KUVP 11472).

Nesophontes Cave: maxillae (1 partial left—USNM 259183); vertebrae (1 dorsal, 2 caudal—USNM 259183).

Cueva de Silva: femora (1 right, 1 left—KUVP 11572).

Barahona IV: vertebrae (2 dorsal, 1 caudal—USNM 259189).

Description.—Dentary: fossil dentaries of *Cyclura pinguis* are not common. From Blackbone 1 there are two fragments each of a left and right dentary which appear to be from jaws broken approximately in half. The pieces consist of the tooth-bearing portions of the bone; the ventral faces are missing. The anterior portion of the right dentary is 30.5 from the rounded symphysis to the broken posterior edge. The posterior half is 34.4 from the broken anterior end to the posterior tip of the articular surface of the coronoid. Thus, the two pieces represent a jaw at least 65 in total length. I doubt that much of the middle portion of the dentary is missing, although the two halves do not join neatly together (Fig. 15). Sixteen teeth or empty alveoli are present on the anterior piece and 14 on the posterior. Avery and Tanner (1971) gave a tooth count of 22 to 28 for *Cyclura*. A recent skeleton of *C. pinguis* (ASFS V21995) with a dentary tooth row of 34.4 has 26 teeth. Thus, accounting for the 2 or 3 teeth missing from the middle piece of the fossil dentary, its tooth count would be about 32—a figure not unreasonable considering the size of the jaw.

The two pieces of a left dentary are proportionately the same size as the aforementioned right hand pieces, but they are smaller and can not be identified as confidently as a single jaw in two pieces. The anterior portion is 23.1 in length. The posterior fragment, bearing an articular facet for the coronoid, is 35.6 in total length. Overall, the jaws are smooth and penetrated by seven foramina anteriorly.

A small right dentary fragment from Cueva del Perro is missing the posterior fourth of the bone. The fossil is 26.5 measured ventrally from the symphysis to the broken posterior edge. The dental shelf extends back only half the length of the bone thus exposing Meckel's canal posteriorly. Six teeth are present out of 13 alveoli on the shelf.

The teeth of *C. pinguis* are high and narrow. The first five or six are simple and pointed. The crowns of the posterior teeth have two small anterior cusps, a large central cusp, and a single small posterior cusp. The crowns also are compressed and oriented obliquely so that adjacent teeth overlap one another. The crowns are moderately expanded beyond the width of the bases, but not to the degree obtained by some species, for example, *C. carinata* and *C. cychlura*. In *C. cornuta* and *C. nubila* the crowns are multicuspate and approach the serrated condition of *Iguana* and *Ctenosaura*. The tooth crowns of *C. pinguis* are in a horizontal plane throughout the length of the dentary, but the bases sit in a concave shelf so that the tallest teeth are in the middle of the dental series. The sides of the teeth are parallel and the shafts are compressed distomesially.

Maxilla: a large, right maxilla from Blackbone 1 could be from the same individual represented by the right dentary discussed above. The bone is broken near the midpoint. The anterior piece is 17.1 in length. It bears the premaxillary process, the anterior half of the nasal process, and a dental row with implacements for eight teeth of which numbers 2, 3, 5 and 7 are present (Fig. 15). The premaxillary process is broad dorsally, 9.0 wide, and has articular surfaces for the premaxilla anteriorly and the vomer anteromedially. The nasal process rises sharply. At its basal curvature is a deep pit leading to the anterior inferior alveolar foramen. The nasal process rises 23.0 above the parapet of the jaw.
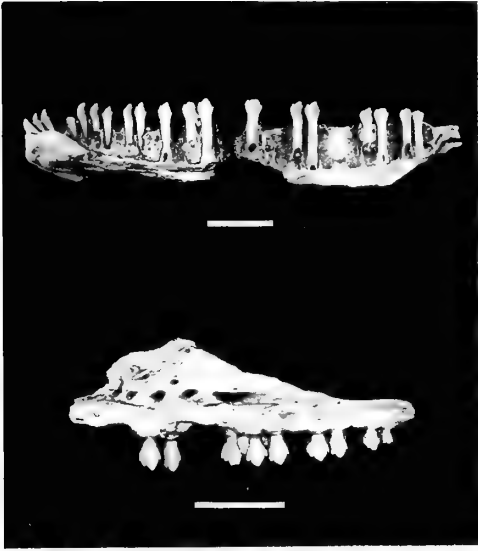
The posterior piece is 39.7 from its

Fig. 15.—Fossil jaws of *Cyclura pinguis*. Lingual view of broken dentary (top, USNM 259158) and labial view of partial maxilla (bottom, USNM 259160). Scale equals 10 mm.

broken anterior edge back to the tip of the pterygoid process. Part of the nasal process is present, but it is missing the dorsal margin. The labial surface is vertical and penetrated by three large and closely spaced foramina located in a row above the parapet of the jaw. The dental shelf is concave with spaces for 16 teeth, 9 of which are present. The lingual edge of the dental shelf produces a medially directed process for articulation with the palatine. The dental shelf narrows fore and aft to either side of the process.

Maxillary teeth are similar to those on the dentary. If, in fact, the two halves are from the same maxilla, then the bone would have had a total length of approximately 59 and a tooth count of 27 or 28.

A small left maxilla, also from Blackbone 1, is missing the anterior edge of the premaxillary process and the posterior expansion of the nasal process. Evidently it is from a juvenile. The bone is 23.5 in length and has 17 teeth or empty alveoli. The teeth are proportionately shorter than those of adults. A

fragment of a left maxilla from Nesophontes Cave consists of the premaxillary process and a dental shelf bearing four teeth and three empty alveoli. It is similar to the large specimen from Blackbone 1.

Premaxilla: a single premaxillary bone from Blackbone 2 is complete, but for the end of the right maxillary process. The bone is large and robust, 31.3 from the anteroventral edge to the tip of the nasal process. The width is 16.6 accounting for the missing right maxillary process. The bone is rounded anteriorly and perforated by numerous small foramina. Four teeth alternate with four empty alveoli. The teeth are simple and pointed. The nasal process is long and thin relative to some species such as *C. cychlura* and *C. nubila* in which it is short and wide. Ventrally, the caudal half of the nasal process is compressed laterally into a keel which articulates with the nasal bones.

Articular and surangular: the left articular from Blackbone 2 and the left surangular from Blackbone 1 are the only bones present from the post-coronoid section of the lower jaw. Both bones are impressively large and came from mandibles probably exceeding 120. The articular is broken anteriorly, but otherwise complete. It is 46.5 long and 24.3 across the tips of the angular and retroarticular processes. The angular process is thick and extends medially 12.7 from the rim of the articular condyle. The large surangular is missing part of the ventral edge. It is 44.8 in length and 12.2 in height. On the anterolabial side is a faint V-shaped depression marking the site of dentary overlap.

Palatine: a right palatine was recovered from the rear wall of San Miguel Cave. The bone is broad, elliptical in shape, and has a well developed vomerine process directed craniad from the anteromedial side (Fig. 16). The length of the bone is 36.5 as measured from the tip of the vomerine process to the curved, posterior border. The greatest width is

19.5 from the lateral edge of the maxillary process straight across to the medial side of the bone. There is a crescent-shaped excavation on the anterolateral surface. Posteriorly, an oblique scar marks the articular surface of the pterygoid.

Pterygoid: two right pterygoids referred to this lizard are both from San Miguel Cave. Each is missing a small anterior portion of the palatine process. They are nearly equal in size, but the larger of the two is 45.0 in length (Fig. 16). The pterygoids of *C. pinguis* are distinguishable from other members of the genus by two features. First, the medial border anterior to the transverse maxillary process is nearly straight with little or no emargination. Secondly, the pterygoid teeth occur in double rows that begin in the middle of the bone at the level of the maxillary process. The rows curve inward along the medial border of the bone and continue craniad as a single row that ends near the apex of the palatine process. More than 20 socketed teeth may be present. The pterygoid tooth pattern of *C. pinguis* closely resembles that of *Iguana* or *Ctenosaura*, but in other species of *Cyclura* the pterygoid teeth occur in a small patch or row and are confined to the middle of the bone. They are usually 10 or less in number. Caution is advised in using this character in iguanine lizards because pterygoid teeth may be variously lost or increased in number with ontogeny. However, the pattern in *C. pinguis* is so distinctive relative to other members of the genus as to be diagnostic.

Parietal: three fossil parietals of different sizes exhibit the ontogenetic variation typical of this bone in many iguanid lizards (see Etheridge, 1959; Oelrich, 1956). As measured across the frontal border, the largest (from Blackbone 2) is 39.5, the smallest (from Blackbone 2) is 27.6, and the intermediate size (from Cueva Clara) is 32.4. As parietals increase in size, the midsagittal ridge heightens and the sides lateral to the ridge become constricted. The angle formed by the supratemporal processes increases as the processes themselves lengthen. In all three fossils the anterior face of the dorsal surface is moderately rugose.

Basale: a large braincase from Blackbone 2 consists of fused exoccipitals, basioccipital and basisphenoid (Fig. 16). The distance is 36.6 between the ends of the exoccipital processes. The generic differences in braincases among iguanine lizards was first pointed out by Boulenger (1890) and later used by Etheridge (1964a) to identify a fossil basale from Barbuda, British West Indies. In *Iguana* and *Cyclura* the basisphenoid is much wider than long and slightly constricted behind the pterygoid processes. In these lizards, the basisphenoid length as measured from the bone's posterior border to the apex of the excavation between the parasphenoid process and the pterygoid process divided by the narrowest width behind the pterygoid process, gives a ratio of 0.40 to 0.72. The ratio of the Blackbone 2 specimen is 0.50 (Fig. 16). In *C. pinguis* the pterygoid processes are broad and short such that the depressions immediately posterior to the processes are shallower than in other species of the genus.

Quadrate: the left quadrate from Blackbone 1 is 23.5 from the apex of the cephalic condyle to the bottom of the mandibular condyle. The bone is rectangular and 14.4 between the lateral and medial borders. Its most unusual characteristic is a prominent shelf which overhangs the quadrate foramen. I have not seen this feature in other species of *Cyclura*.

Limb bones and girdle elements: many appendicular components of varying sizes are present as fossils. There is nothing remarkable about these bones that would distinguish them from the same elements of other species of *Cyclura*. They are more useful for estimating animal size and minimum number of individuals per locality. Most of these

fossils are missing proximal or distal ends, epiphyses, pieces of the shafts or combinations of these. Measurements of the longest and shortest complete long bones are, as follow: humeri 75.9, 33.9; ulnae 61.8; radii 57.2, 54.3; femora 80.0, 53.2; tibiae 69.8, 25.8; fibulae 72.0, 63.9. A single ilium and pubis have lengths of 49.3 and 15.9, respectively.

Comments.—The occurrence of rock iguanas on Puerto Rico was first revealed by Barbour (1919:97) from a description of fossils found ". . . in a large cave near Ciales." The fossils were collected two years previously by G. M. Allen and J. L. Peters. Barbour chose the broken extremities of a left humerus as the holotype (MCZ 1008) and named the species *Cyclura portoricensis.* He used limb bones in order to compare them with the holotype of *C. mattea,* a left humerus (USNM 59358-9) described by Miller (1918) from Indian middens at Magens Bay, St. Thomas, Virgin Islands. *Cyclura portoricensis* was distinguished from *C.*

mattea by being larger and more massive. Barbour thought that *C. portoricensis* and *C. mattea* were more closely related to one another than either was to the living *C. pinguis* on Anegada Island at the eastern extreme of the Puerto Rican Bank. Barbour also believed that *C. portoricensis* resembled *C. cornuta* in having a shallower radial fossa than that of *C. mattea.* Limb elements of iguanine lizards are poor indicators of species-level taxonomic differences because of their relative simplicity, ontogenetic change, individual variation, and sexual dimorphism by size. I examined the holotypes and paratypes (all limb bones) of both *C. portoricensis* and *C. mattea* and, except for size differences, found nothing significant that would differentiate them from *C. pinguis* or from any other species of *Cyclura.*

The presence of three species of *Cyclura* on the Puerto Rican bank is, and has been, considered unlikely (Schwartz

Fig. 16.—Fossil skull bones of *Cyclura pinguis.* Left, basale (top, occipital view, bottom, ventral view, USNM 259174); right top, right palatine in ventral view (USNM 259186); right bottom, right pterygoid in ventral view (USNM 259184). Scale equals 10 mm.

and Thomas, 1975; Schwartz and Carey, 1977), but until now adequate fossil material from the islands that could verify or refute the contention was unknown. The fossils discussed here clearly are referrable to the species of Anegada Island. Of the three available names, *portoricensis, mattea,* and *pinguis,* the latter has priority. Bones with osteological characters that are considered diagnostic for the species include the pterygoid, basisphenoid, dentary, and maxillary teeth, and the palatine, quadrate, and nasal processes of the premaxilla. In their review of iguanine lizards, Avery and Tanner (1971) suggested that *C. carinata, C. cornuta,* and *C. nubila* (= *C. macleayi*) are typical of the genus. My examination concurs in that most species of *Cyclura* are difficult to separate osteologically except for *C. pinguis.* Externally, *Cyclura pinguis* is also one of the most distinctive members according to Schwartz and Carey (1977), who reviewed the genus and relegated several Bahaman forms to subspecies, reducing the previously recognized number of species from 14 to 8.

Cyclura pinguis is the most southerly occurring species of this West Indian genus. (A fossil basale from Barbuda, British West Indies *may* belong to *Cyclura;* see Etheridge, 1964a.) *Cyclura pinguis* is restricted to xeric habitats in and around rock outcrops (Carey, 1975) like its northern congeners, *C. nubila* (Cuba, Cayman Islands), *C. cychlura* (Bahamas), *C. carinata* (Turks and Caicos Islands, Bahamas), *C. collei* (Jamaica), *C. cornuta* (Hispaniola, Mona Island), *C. ricordi* (Hispaniola), and *C. rileyi* (Bahamas). *Cyclura pinguis* is also one of the largest members of the genus—males to 539, females to 476 snout-vent length. Fossil individuals ranged from juvenile to adult in size. The smallest, based on a femur was 130-140, whereas the largest exceeded 560 based on skull bones, vertebrae, and limbs.

Leiocephalus

The iguanid lizard genus *Leiocephalus* is endemic to the West Indies and almost restricted to the Greater Antilles. Cuba, Hispaniola, and the Bahamas harbor 20 of 21 living species. *Leiocephalus herminieri* is known only from four specimens with questionable locality data on Martinique. It may be extinct. Two of three species known only as fossils extend the former range of the genus to Jamaica (*L. jamaicensis,* Etheridge, 1966a), and Barbuda in the Lesser Antilles (*L. cuneus,* Etheridge, 1964a). The third extinct form, *L. apertosulcus,* was described from Hispaniola (Etheridge, 1965).

Most iguanid lizard genera exhibit multicuspid tooth crown morphology, but flared, fan-shaped tricuspid teeth are diagnostic of *Leiocephalus.* The large iguanines, *Iguana, Cyclura, Ctenosaura, Conolophis,* and *Amblyrhynchus* differ in having deeper jaws and detailed tooth crowns. Anolines lack fan-shaped tooth crowns and an anterior opening for Meckel's canal. *Leiocephalus* and *Leiolemus* are the only lizards possessing fan-shaped tricuspid teeth, a closed Meckelian groove open anteriorly, and an anterior extension of the coronoid on the labial surface of the dentary (Etheridge, 1966b; Estes, 1963). In most species of *Leiolemus,* the lateral cusps are not as well delimited from the central cusp as they are in *Leiocephalus.* Also, in some species of *Leiolemus* such as *L. elongata, L. multiformis,* and *L. nitidus,* the splenial extends farther anterad than in any *Leiocephalus,* spanning seven or eight teeth, whereas the maximum in *Leiocephalus* is three or four.

Finding fossil *Leiocephalus* on Puerto Rico was not wholly unexpected because of its past and present distribution, although none is living there now. Two extinct species are present as fossils. One is represented by skull and postcranial elements and the other species by two dentaries. Both possess the characters of the genus. Richard Etheridge

first recognized the differences between insular and mainland lizards previously referred to *Leiocephalus*. Moreover, by his contribution to the herpetology of the West Indies, and our friendship which partly inspired this study, it is gratifying to name the first of these two lizards:

Leiocephalus etheridgei, new species

Holotype.—A right dentary No. 259190 in the vertebrate paleontology collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Type locality and horizon.—Blackbone 1 Cave, 1.2 km S Barrio de Barahona, Municipio de Morovis, Puerto Rico (18° 20′ 57″ N, 66° 26′ 47″ W). Late Pleistocene.

Material.—Blackbone 1: dentaries (7 right, 5 left, 5 fragments—USNM 259190-1); maxillae (1 right, 1 fragment —USNM 259192); frontals (3—USNM 259193-4); basales (4—USNM 259195-7); basisphenoids (1 fragment—USNM 259198); pterygoids (1 left—USNM 259202); dorsal vertebrae (10—USNM 259199); sacral vertebrae (8—USNM 259200); caudal vertebrae (2—USNM 259201).

Cuevo del Perro: dentaries (1 right, 6 left—KUVP 11473).

Diagnosis.—*Leiocephalus etheridgei* is distinguished from all known species of the genus by the presence of an acute convex ridge on the anterior, labial face of the dentary below the mental foramina, and by the anterior opening of Meckel's groove, which extends from the level of the sixth tooth forward to the symphysis of the jaw. In other species of *Leiocephalus* the labial face of the dentary is smooth and convex, and but for *L. apertosulcus*, Meckel's groove is open anteriorly as a small pore beneath the first or second tooth. In *L. apertosulcus* Meckel's groove is open and unfused throughout the length of the dentary (Etheridge, 1965).

Description.—The holotype (Fig. 17)

is a nearly complete right dentary measuring 13.6 mm from the symphysis posterior to the broken tip of the angular process. It came from an individual with an estimated snout-vent length of 110-115 mm. The tooth row has a straight-line measurement of 11.8 mm and contains 20 pleurodont teeth or empty alveoli. Teeth missing from front to back are numbers 1, 2, 6, 8, 11, 16, and 19. The height of the dentary just posterior to the last tooth is 3.0 mm. The anterior upper half of the labial face is smooth and concave. Posteriorly the labial face is slightly convex. The anterior upper half of the labial face is demarcated from the lower half by a narrow, convex ridge arching gently from the symphysis posteriorly to the level of the sixteenth tooth. Nine foramina of unequal size are spaced irregularly on the labial face between the second and thirteenth teeth. Posteriorly there is a faint wedge-shaped coronoid scar that extends forward to the level of the last tooth. The ventral surface of the dentary is flat anteriorly, but slightly convex posteriorly. Meckel's groove is open at the front of the jaw as a lanceolate cleft extending from the level of the sixth tooth forward to the symphysis. Lingually, the bone is smooth and convex below the tooth row except for a shallow, longitudinal depression preceding the posterior opening of Meckel's groove, which remains open posteriorly to the level of the sixteenth tooth.

The crista dentalis has a ventral curvature deepest at the midpoint of the jaw. Accordingly, the teeth are largest in the center of the dental row and become smaller fore and aft. The bases of the teeth are cylindrical except for the posterior three which are mesodistally compressed. The tricuspid crowns are broader than the bases and have sharp linguilabially compressed cutting edges. The central cusps are pointed, higher, and larger than the lateral cusps, and separated from them by grooves extending to the base of the crown. Weakly developed lateral cusps are present on

the third tooth and are fully developed on the fourth tooth and all others but the last. The last tooth is nearly conical because the lateral cusps are rudimentary. About 40% of each tooth is exposed above the jaw parapet.

The other dentaries from Blackbone 1 and Cueva del Perro are similar to the holotype. Tooth row lengths of 16 fossils vary from 9.3 to 12.5 mm ($\bar{x} = 11.0$). Teeth missing from the holotype are variously present in the referred specimens, except for the second tooth, and are similar to others in the tooth row. Small, pointed replacement teeth are present in several dentaries.

Maxilla: one maxilla and one maxillary fragment from Blackbone 1 are referred to this species. The more complete specimen (Fig. 18) is missing the dorsal end of the nasal process. Its total length is 12.4 mm and it measures 11.4 mm along the tooth row. The bone contains 18 teeth or empty alveoli. Missing from front to back are numbers 7, 12, 15 and 17. Parts of the bases of teeth 3, 5, and 9 are missing also. The first tooth is simple and pointed and the second tooth is weakly tricuspid. All teeth posterior to number 2 are flared and tricuspid like those of the dentary. The crowns are oriented at an oblique angle such that the anterior cusp of each tooth overlaps the lingual surface of the posterior cusp on the preceding tooth. The labial face of the maxilla is smooth and penetrated by an irregular series of 15 foramina.

The maxillary fragment is an anterior piece bearing the premaxillary process, part of the nasal process, and a section of the dental row with seven teeth or empty alveoli. The third, fifth, and seventh teeth are replacement series, smaller and narrower than those that are fully developed.

Frontal: two frontal bones, one large and one small, are typical of *Leiocephalus* in being broad at the parietal border and constricted medially. The larger specimen is missing the tip of the left supratemporal process (Fig. 18). It is 12.7 mm as measured midsagitally, 11.7 mm across the parietal border, 4.8 mm across the narrow midsection, and 6.1 mm at the anterior end. The pineal foramen is present on the parietal border as a V-shaped notch. The bone has a slight dorsal curvature and an irregularly sculptured surface. There are two dorsal, semicircular depressions for articulation with the nasal bones on the anterior border. Laterally the frontal is thick and rounded and bears prefrontal scars extending back half the length of the bone. The smooth ventral surface has two low descending laminar processes and a notch anteriorly for articulation with the nasals.

The smaller frontal bone is missing the tips of the supratemporal processes and the ends of the nasal processes. The bone is 9.0 mm long, 6.7 mm across the parietal border, 2.9 mm across the middle and 4.2 mm wide at the anterior end. It is otherwise similar to the larger specimen.

Basale: *Leiocephalus etheridgei* also is represented by four braincases each composed of fused exoccipitals, a basioccipital and basisphenoid. The two most nearly complete specimens are 12.3 mm and 11.8 mm across the exoccipitals and 6.5 mm and 6.3 mm from the anterior border of the parasphenoid to the posterior lip of the occipital condyle. The other two basales are missing portions of the basisphenoid and basioccipital. They are 12.2 mm and 10.6 mm across their respective exoccipital processes. The pterygoid processes on the complete basales are long, and flare out laterally so that their distal ends are in a line with the sphenoccipital tubercles.

Fɪɢ. 17.—Holotype of *Leiocephalus etheridgei*, new species (top, dentary in lingual and labial views, USNM 259290), and holotype of *L. partitus*, new species (bottom, dentary in lingual and labial views, USNM 259203). Scale equals 5 mm.
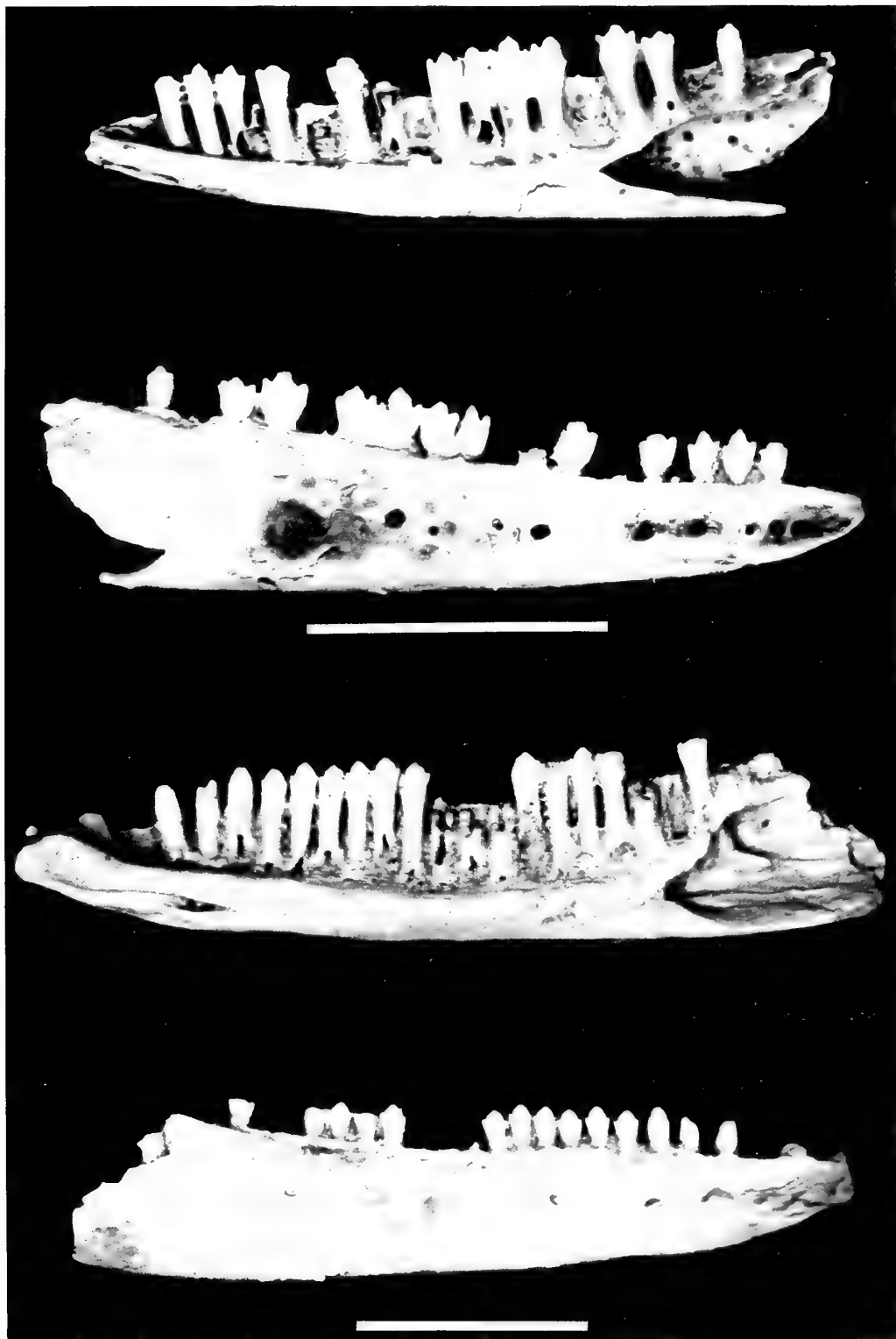
The sutures are fused between the respective bones of each braincase. One fossil is shown in Figure 18.

Vertebrae: vertebrae are referred to this species on the basis of their size and similarity to those of other species of *Leiocephalus*. They are from various regions of the vertebral column. The largest midbody vertebra has a centrum 2.7 mm in length, including the condyle, and bears a midventral ridge. The neural spine is robust and angles posteriad to a height of 1.9 mm. Zygosphenes are moderately developed within the anterior rim of the neural arch. Hypopophyses are present on the cervical vertebrae. Eight sacral vertebrae of nearly equal size have an average width across the diapophyses of 9.5 mm. Two preautonomic caudal vertebrae are 6.1 mm and 6.4 mm across their diapophyses. They have well-developed zygosphenes.
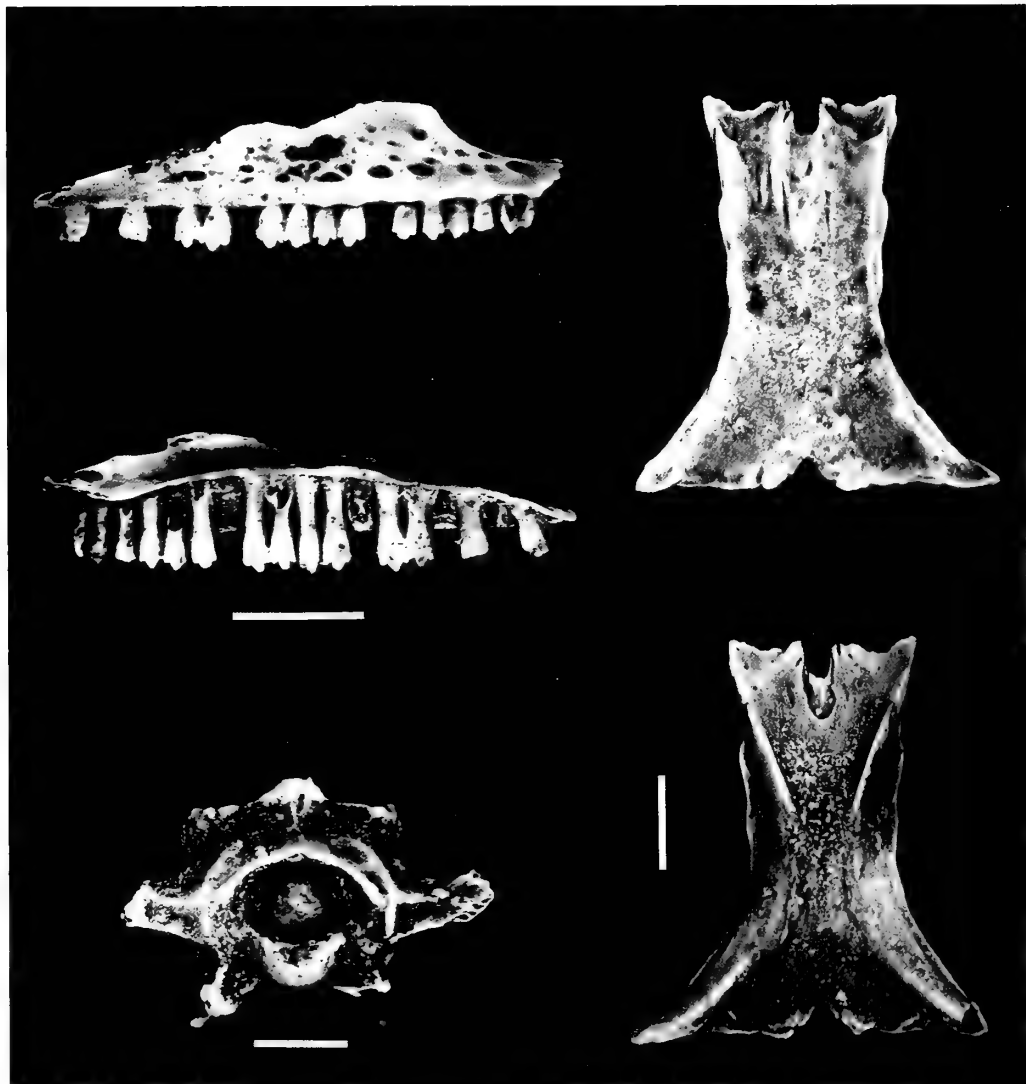

FIG. 18.—Fossils of *Leiocephalus etheridgei,* new species. Maxilla (top left—lingual and labial view, USNM 259192); basale (bottom left—occipital view, USNM 259196); frontal bone (top right—dorsal view, bottom right—ventral view, USNM 259193). Scale equals 3 mm.

Leiocephalus partitus, new species

Holotype.—A right dentary No. 259203 in the vertebrate paleontology collection of the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Type locality and horizon.—Guánica Bat Cave, Reserva Forestal Guánica, 6 km E Barrio de Guánica, Municipio de Guayanilla, Puerto Rico (17° 57′ 40″ N, 66° 50′ 53″ W). Late Pleistocene-Sub-Recent.

Material.—Guánica Bat Cave: dentaries (1 right—USNM 259203).

Cueva del Perro: dentaries (1 right —KUVP 11473).

Diagnosis.—A large species of *Leiocephalus* distinguished from all other members of the genus by the presence of a vertical intramandibular septum traversing the length of Meckel's groove and fused to the ventral, internal surface of the dentary. An intramandibular septum of this proportion is not present in any other species of *Leiocephalus* in which Meckel's groove is closed. *Leiocephalus partitus* is further characterized by blunt, weakly flared tricuspid teeth, the transition to tricuspid teeth taking place at a more posterior position in the tooth row and by Meckel's groove opening anteriorly below the seventh tooth.

Etymology.—*partitus*, L. divided; in reference to the intramandibular septum.

Description.—The holotype (Fig. 17) is a nearly complete right dentary that came from an individual with an estimated snout-vent length of 125-130 mm. The bone is missing the posterior border behind the coronoid scar. The dentary is 16.2 mm in total length and has a tooth row of 13.5 mm measured in a straight line. There are 24 teeth or empty aveoli of which the following teeth are missing from front to back: numbers 2, 4, 14, 15, 16, the base of 17, and the crowns of 21 and 24. The height of the dentary is 3.5 mm just posterior to the last tooth. The first tooth is oriented anterodorsally as a simple shaft with a pointed crown. The third tooth is larger

and missing the crown, but otherwise is similar to the first. The still larger fifth, sixth, and seventh teeth are also simple and pointed. The transition to tricuspid teeth begins with the eight tooth which has rudimentary lateral cusps adjacent to a blunt median cusp. The ninth and all posterior teeth have tricuspid crowns. The tooth bases are mesodistally compressed. The crowns have a slight lateral flare only and are not appreciably wider than their bases. Lateral cusps are separated from the median cusps by shallow furrows extending to the base of the crown. The median cusps are blunt points; thus, the shearing surface of the tooth row is not so acute as it is in other species of *Leiocephalus*. In occlusive view, the tooth row presents a reversed sigmoidal outline; the row curves laterally from the symphysis, back medially towards the middle of the row and then laterally again posteriorly.

The upper half of the labial face is smooth and convex except for an irregular surface anteriorly. A horizontal row of five mental foramina penetrates the labial surface between the second and fourteenth teeth. There is a large >-shaped scar for the coronoid overlap on the upper posterior surface. The scar extends forward to the level of the twentieth tooth. The lower half of the labial face is convex anteriorly and flat posteriorly below the coronoid scar. The ventral surface is rounded. Meckel's groove opens as a narrow pore below the level of the seventh tooth on the ventral surface and continues forward to the symphysis as a deep, curving sulcus. The dental shelf is produced lingually as a horizontal ledge upturned at the front of the bone. The shelf curves dorsally at the level of the twentieth tooth with the widening of Meckel's canal. At this widening an intramandibular septum is exposed as a vertical partition within the canal. The ventral border of the septum is fused to the dentary and extends back to the last tooth.

The only other bone referred to this

species is another right dentary recovered from Cueva del Perro, estimated to have come from a lizard with a snout-vent length of 120 mm. It is very similar to the holotype, but with the following measurements: total length 14.7 mm; tooth row length 13.3 mm; and height 2.9 mm posterior to the last tooth. The dentary has 24 teeth or empty alveoli of which numbers 5, 7, 15, 22 and 24 are missing. The first four teeth as before are simple and pointed like the first tooth of the holotype. The transition to tricuspid teeth begins at the tenth tooth and is completed at the eleventh. A well-developed intramandibular septum also is present in this specimen.

Comments.—There are no extant species of *Leiocephalus* with dentary characters approaching those of *L. etheridgei* or *L. partitus.* The Cuban lizard *L. macropus* has a labial ridge like that of *L. etheridgei,* but it is poorly developed and the dentary has fewer mental foramina (5 versus 9). In fact, the dentaries of living species of *Leiocephalus* are uniform and morphologically comparable. Variations and similarities of features such as tooth-crown shape probably reflect dietary specializations, whereas other characters may have phylogenetic significance such as the anterior condition of Meckel's groove. The opening is wide and uniform to the end of the jaw in *L. etheridgei,* whereas in *L. partitus* the opening is small and continues craniad as a narrow sulcus. But in both Puerto Rican species the opening is at about the same place on the jaw—much farther posterior than in other *Leiocephalus.* This probably reflects incomplete fusion of Meckel's groove, and to this extent *L. etheridgei* and *L. partitus* approach the condition of *L. apertosulcus* in which the groove is open altogether. Complete fusion of Meckel's groove occurs in a number of iguanids, but sporadically among lizards in general. Thus, the fusion of Meckel's groove is derived for *Leiocephalus* and in other iguanids

where it occurs, and the open condition of *L. apertosulcus* and incomplete fusion in *L. etheridgei* and *L. partitus* is primitive for *Leiocephalus* and not necessarily indicative of relationships amongst these three species. Most species of *Liolaemus* show fusion of Meckel's groove with an anterior opening similar to *Leiocephalus,* but there is also incomplete closure and fusion in several species, for example, *Liolaemus lineomaculatus, L. fitzingeri, L. kingi,* and *L. wiegmanni.*

An intramandibular septum is absent from *Leiocephalus etheridgei* and *L. jamaicensis,* but is prominent in the other fossil species *L. apertosulcus* and *L. cuneus.* In these two, the structure is similar to that of *L. partitus* except that the posterior edge is distinctly emarginate. The septum is absent from other representative tropidurines (*sensu* Etheridge, 1964b:629) such as *Tropidurus torquatus, Plica umbra, Stenocercus varius, Uranoscodon superciliosa,* and *Uracentron flaviceps.* A short septum is present in *Ophryoessoides iridescens,* several species of *Liolaemus (multiformis, chilensis, nigriceps, lineomaculatus)* and some modern species of *Leiocephalus (carinatus, melanochloris, schrebersei, punctatus).* In these species the septum is "short" in that it does not extend posteriorly for more than three-fourths of the length of the dentary, and the nutrient canal it forms by fusing to the inner labial wall has a very small diameter. The septum may continue aft as a short keel descending from the roof of Meckel's canal. There is an interesting sequence in the reduction of the septum that corresponds with closure of Meckel's groove in *Liolaemus.* Closure of Meckel's groove increases along the length of the dentary from *L. multiformis* to *L. chilensis* to *L. nitidus,* and the septum becomes fused more to the inner labial wall rather than the ventral floor, in other words a more horizontal as opposed to vertical orientation within the dentary. Perhaps then, the absence of an intramandibular septum in other tropidurines is a loss

resulting from the closure and fusion of Meckel's groove, *Leiocephalus cuneus* and *L. partitus* being exceptions.

There is more to the above argument, however. The intramandibular septum is not common in iguanids, whether Meckel's groove is open or closed, and where present, it is reduced, extending no more than half to three-fourths of the length of the dentary. Among iguanines, lizards in which Meckel's groove is fused, the septum is best developed within *Ctenosaura* and least in *Conolophis*. *Iguana*, *Cyclura*, and *Dipsosaurus* are intermediate. A septum like that of the iguanines is present in *Sceloporus* and *Urosaurus*, the sceloporines that I examined, and Meckel's groove is either open or mostly unfused in this group (Etheridge, 1964b). The septum is absent from most anoles, but it is present as a very thin structure in the giant species *A. cuvieri*, *A. ricordi*, and *A. equestris*; Meckel's groove is completely fused in all *Anolis*.

In anguimorph lizards, Estes (1964: 124) correlated the intramandibular septum with dentary/post-dentary articulation, but the morphology of the septum in these lizards suggests that this septum might not be homologous with that of iguanids. However, the septum, or some remnant of it, does play a part in dentary/post-dentary articulation in iguanid lizards. In large iguanines (*Iguana*, *Cyclura*, *Amblyrhynchus*, *Ctenosaura*, *Conolophus*), *Laemanctus*, *Basiliscus* (basiliscines), *Morunosaurus*, *Enyaliosaurus*, and *Enyalioides* the articulation is a vertical ziz-zag joint between the dentary and surangular-angular on the labial side of the jaw directly below the coronoid. The intramandibular joint is a tongue and groove arrangement in which the surangular laterally and the anterolingual arm of the coronoid medially form a slot, into which fits the short, posterior keel of the intramandibular septum descending from the inner roof of the dentary. In these lizards, except the basiliscines, the joint is reinforced by a pronounced an-

teriorly directed overlap of the coronoid onto the labial surface of the dentary, forming a bracket on top of the jaw. In *Laemanctus* and *Basiliscus*, where the tongue and groove arrangement is more robust, the labial arm of the coronoid descends vertically onto the mandible, mostly overlapping the surangular.

In *tropidurines* and *Anolis* the intramandibular joint is a modification of the above condition. The most conspicuous difference is that in tropidurines and *Anolis* the labial surface of the dentary extends posteriorly beyond the middle of the coronoid, about 10-12% of the dentary length on the average. In these lizards the primary joint is provided, by the wide overlap of the posterior end of the dentary onto the surangular bone, with an articulation which may fuse in adults. On the lingual side of the jaw, the anterolingual arm of the coronoid fits up underneath the overhanging dental shelf flush against the surangular. Presumably, this articulation is a condition derived in conjunction with the reduction of the splenial in these lizards. When the intramandibular septum is present, as in those species mentioned previously, the joint is still formed the same way; the keel fits flush on top of the anterolingual arm of the coronoid. The coronoid overlaps the dentary on the labial surface in *Anolis*, but not in tropidurines except *Leiocephalus*, *Liolaemus*, and, to a slight extent, in *Ctenoblepharis*.

In *Sceloporus*, the intramandibular joint is structurally intermediate to the "iguanine" type and the "tropidurine" type. The surangular and the anterolingual arm of the coronoid form a slot to receive the descending keel of the intramandibular septum. There is no coronoid overlap on the labial side of the jaw, but the dentary does extend posteriorly beyond the level of the coronoid to form a fairly wide overlap with the surangular, though not as much as in tropidurines and anoles.

We might conclude that whereas the

significance of the intramandibular septum in iguanids is unclear, the structure is present primitively as a weakly developed feature in most members of the family; its loss altogether is loosely correlated with closure and fusion of Meckel's groove. Thus, the hypertrophied condition of the intramandibular septum in *Leiocephalus partitus*, *L. apertosulcus* and *L. cuneus* is a uniquely derived state suggesting a relationship between these three species.

The number of dentary teeth increases with tooth row length in *Leiocephalus*, as it does in many lizards, but for individuals of equivalent size the number is fairly constant among species. The fewest teeth occur in *L. macropus* (18) and the greatest number in *L. melanochloris* (25). Twenty-two is average. Likewise, the transition from simple to tricuspid teeth takes place rather abruptly between the seventh and ninth teeth except for the species *L. cuneus*, *L. etheridgei*, and *L. partitus*. In the former two, the transition is completed at the fourth or fifth tooth and in *L. partitus* at the tenth or eleventh tooth. The more anterior transition to tricuspid teeth was used by Etheridge (1964a) to distinguish *L. cuneus* from other species of *Leiocephalus*. Although *L. cuneus* now shares this character with *L. etheridgei*, the former species has an intramandibular septum, a deeper coronoid scar which extends farther forward on the labial surface of the jaw, and a smaller anterior opening for Meckel's groove.

The anterior coronoid overlap does not reach the last tooth in the species *barahonensis*, *macropus*, *pratensis*, and *semilineatus*. The overlap reaches the last tooth in *etheridgei*, *inaguae*, *greenwayi*, *loxogrammus*, *raviceps*, *stictogaster*, and *vinculum* and extends to the penultimate tooth or beyond in *carnatus*, *cuneus*, *cubensis*, *lunatus*, *melanochloris*, *psammodromus*, *punctatus*, and *partitus*. There is little correlation with this character and the anterior extent of the

splenial on the lingual side of the jaw. The splenial does not reach the level of the last tooth in *L. macropus*, but spans the posterior three or four teeth in *carinatus*, *melanochloris*, *personatus*, *punctatus*, *psammodromus*, and *raviceps*. The splenial overlaps one or two teeth in all other species. The anterior extent of the splenial does not appear to be size-related because in the small Cuban species, *L. raviceps*, the bone spans three posterior teeth as it does in the larger *L. carinatus*. The splenial is absent from the fossils, but the scar remains on the posterodorsal edge of Meckel's groove. The scar extends for three teeth in *L. partitus* and for four in *L. etheridgei*. Finally, the anterior inferior alveolar foramen and the mylohyoid foramen are joined as a single opening in about half the species. However, this feature may be subject to ontogenetic change.

Examination of dentary characters reveals features that easily distinguish the fossil species *L. etheridgei*, *L. partitus*, *L. apertosulcus*, and *L. cuneus* from the extant forms and, in fact, the latter three extinct species may be related on the basis of the enlarged intramandibular septum. However, there is more difficulty in distinguishing the living forms from one another. Osteological features can be useful for identifying species, but apparently they are too subtle to show relationships within the genus. This point is demonstrated further by lizard fossils recently discovered from the middle Miocene of Nebraska, which currently are being described as an extinct species of *Leiocephalus* by Carl Wellstead who kindly provided me with illustrations and descriptions for this discussion. Although this North American species is indeed distinct from any fossil or recent West Indian member of the genus, the differences are within expected morphological variation for these lizards. It appears from the available material, though, that among the trends in the evolution of *Leiocephalus* are: 1) reduction of the angular, 2) narrowing and shortening of

the splenial in its placement within Meckel's groove, 3) posterior extension of the dentary onto the surangular and 4) loss of the intramandibular septum and fusion of Meckel's groove. That these transformations are more evident and complete in other tropidurine genera suggest that, on these characters, *Leiocephalus* is the least derived member of the group.

Scincidae

Mabuya mabouya Lecépède

Material.—Blackbone 1: dentaries (1 right, 4 left—USNM 259205-6); parietals (1—USNM 259207); basales (1—USNM 259208); pelves (1 right—USNM 259209); dorsal vertebrae (31—USNM 259210); sacral vertebrae (1—USNM 259211).

Description.—Two of the five dentaries referred to this species are complete. Their tooth rows measure 8.5 and 8.2 and they have 31 and 28 teeth or empty alveoli, respectively. The larger specimen is shown in Figure 19. The dentaries of *Mabuya mabouya* have smooth and convex labial surfaces. Lingually, the dental row is set in a shallow horizontal trough. Meckel's groove is closed anteriorly, but open for the posterior third of the jaw. On the fossils the articular surface for the splenial is visible throughout most of the dorsal edge of the Meckelian opening. An intramandibular septum is fused internally to the ventral surface of Meckel's canal and extends for three fourths of the dentary length. Teeth are straight and simple with lingually directed, striated, conical cusps.

The other fossils are not remarkable in their comparison with recent skeletal material of *Mabuya mabouya*. The fossil parietal is missing the right nasal process. It measures 4.7 across the posterior border and 4.9 along the left side. The basale is very small, 3.2 in width. The pelvis is missing most of the ischium, but the ilium is complete and 7.2 in length from its distal end to the center

of the acetabulum. All the dorsal vertebrae are similar to one another—with elongate centra and neural arches and long sloping neural spines that extend past the postzygopophyses. The average length of the centra is 2.5.

Comments.—A minimum of five individuals is represented by the fossils, the largest of which had an estimated snout-vent length of 99. The largest of 155 alcohol specimens of this species in the University of Kansas herpetology collection is 105.

Mabuya mabouya occurs on all larger islands and cays of the Puerto Rican Bank and ranges throughout the Lesser Antilles and South and Central America. Little is known of its habits in the West Indies, but the lizard is most often encountered at forest edges near logs and fallen trees in sunny locations. Dunn (1935) made an attempt at subspecific recognition in the island populations. Greer (1970) included the genus in his review of scincid lizard subfamilies in which he elaborated on the osteology of the family.

Teiidae

Ameiva exsul Cope

Material.—Blackbone 1: dentaries (12 right, 9 left—USNM 259212-3); articular + surangular (5 right, 4 left—USNM 259214); coronoids (3—USNM 259218); maxillae (10 right, 10 left—USNM 259215-6); frontals (3—USNM 259219-20); parietals (3—USNM 259221); basales (6—USNM 259222-3); quadrates (2 right, 5 left—USNM 259217); palatines (2 right—USNM 259224); scapulae (9 right, 5 left—USNM 259225); pelves (3 right, 2 left—USNM 259226); atlas (1—USNM 259227); dorsal vertebrae (90—USNM 259227-30); sacral vertebrae (11—USNM 259231); caudal vertebrae (21—USNM 259228).

Cuevo del Perro: dentaries (6 right, 3 left—KUVP 11473); maxillae (1 right —KUVP 11476); parietals (1—KUVP 11473); pelves (2 right, 3 left—KUVP

11475); vertebrae (5 dorsal, 1 sacral, 1 caudal—KUVP 11472).

San Miguel Cave: dentaries (2 right, 2 left—USNM 259241); maxillae (2 right, 2 left—USNM 259242); parietals (1—USNM 259243); vertebrae (1 dorsal, 1 sacral, 3 caudal—USNM 259244).

Blackbone 2: dentaries (1 right, 2 left—USNM 259232); articular + surangular (1 right, 1 left—USNM 259234); pelves (1 right—USNM 259236); interclavicle (1—USNM 259235).

Cueva Clara: dentaries (2 right—KUVP 11526); maxillae (1 right—KUVP 11526); basales (1—KUVP 11564); vertebrae (1 sacral, 1 caudal—KUVP 11564).

Barahona IV: maxillae (1 left—USNM 259245); frontals (1—USNM 259246); parietals (1—USNM 259247); pelves (2 right—USNM 259248); vertebrae (1 dorsal—USNM 259248).

Nesophontes Cave: dentaries (1 right, 1 left—USNM 259237); maxillae (1 right, 1 left—USNM 259238); basales (1—USNM 259239); vertebrae (5 dorsal—USNM 259240).

High Cave: dentaries (1 right—USNM 259249); maxillae (1 right fragment—USNM 259259); vertebrae (1 dorsal—USNM 259250).

Guánica Bat Cave: dentaries (1 right—USNM 259250); articular + surangular (1 left—USNM 259251).

Description.—Fossil dentaries of *Ameiva exsul* are common in occurrence. The bones from all localities are variable in size and exhibit ontogenetic variation. In juveniles and smaller individuals the dental shelf is horizontal throughout the anterior two-thirds of its length. Posteriorly the shelf slopes up with the widening of Meckel's groove. In adults, the dental shelf is horizontal for the anterior half of the bone before Meckel's groove widens. This gives a distinctive arc to the tooth row (Fig. 19). The labial face of the dentary is smooth and gently convex in juveniles, but in adults the posterior margin on the labial side bulges out in a prominent angle at the bottom of the coronoid scar. Sculpturing

in the form of horizontal grooves is present on the ventral surface of dentaries over 20.

Anterior dentary teeth are small and unicuspid. The larger posterior teeth are bicuspid. The transition from unicuspid to bicuspid teeth is variable, but usually occurs between the fifth and tenth teeth. The posterior teeth of juveniles and occasionally the ultimate and penultimate teeth of adults may be tricuspid. Blunt, molariform crowns are present on a few of the largest specimens. In the fossils a tendency exists for an increase in tooth count with lengthening of the dental row up to 17. Tooth counts ranged from 17 to 26 in dentaries 13 to 23 in length. Tooth rows over 17 in length have a mean and mode of 23 teeth.
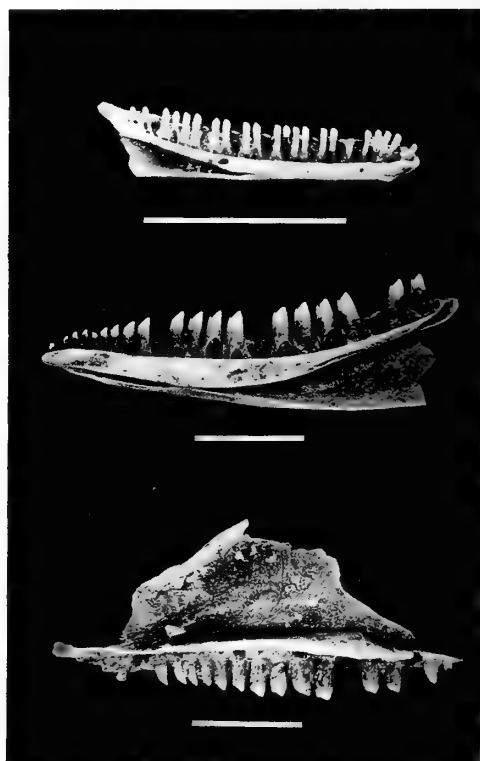
Pertinent dimensions of other fossil

FIG. 19.—Fossils of *Mabuya mabouya* (top, dentary USNM 259205), *Ameiva exsul* (middle, dentary USNM 259212; bottom, maxilla USNM 259216). Scale equals 5 mm.

skull bones are given in Table 4. All are similar to the same bones of *Ameiva undulata parva* described by Fisher and Tanner (1970) and they need not be discussed here. A dentary, maxilla, basale, and frontal are shown in Figs. 19 and 20. Pelvic girdle elements are common in the assemblages and it is worth pointing out their most diagnostic feature. The ilia are short and very robust with high, recurved iliac processes. The acetabulum is deep and both the pubis and ischium are widely expanded distally.

Comments.—*Ameiva exsul* is a conspicuous component of Puerto Rico's modern herpetofauna. The lizard is primarily a beach denizen, although it also is found in sunny, open habitat below 150 m (Heatwole and Torres, 1967). It occurs sympatrically with the other Puerto Rican *Ameiva, A. wetmorei,* which is restricted to the southwest and Isla Caja de Muertos off the coast from Ponce. I was unable to discern osteological differences between these two species other than size, but admittedly my comparative material of *A. wetmorei* was meager. The average snout-vent length of *Ameiva exsul* is 125, but some individuals may reach 200 (Heatwole and Torres, 1967). The average snout-vent length of adult *Ameiva wetmorei* is 50 to 60. The fossils are all from individuals over 60 and I have assigned them to *A. exsul* on this basis. Snout-vent length estimates from various skeletal elements are, as follow: dentaries 134 (92-165), maxillae 123 (94-152), basales 151 (103-194), frontals 128 (116-139), parietals 126 (104-152), scapulae 149 (97-190), sacral vertebrae 118 (102-135).

Anguidae

Diploglossus pleei Duméril and Bibron

Material.—Nesophontes Cave: dentaries (8 right, 5 left—USNM 259258-9); articulars (5 left—USNM 259260); maxillae (3 right, 2 left—USNM 259261-2); frontals (1—USNM 259263); parietals

(2—USNM 259264); basales (1 complete, 2 fragments—USNM 259265-6); pelves (2 right, 4 left—USNM 259267); vertebrae (28 dorsal, 14 sacral, 38 caudal —USNM 259268); osteoderms (15— USNM 259299).

Blackbone 1: dentaries (1 left fragment—USNM 259252); articular (1 right—USNM 259253); maxillae (1 right —USNM 259254); frontals (1 right half —USNM 259255); pelves (1 left—USNM

FIG. 20.—Fossils of *Ameiva exsul.* Basale (top —occipital view, middle ventral view, USNM 259222), frontal bone (bottom—dorsal view, USNM 259220). Scale equals 5 mm.

TABLE 4.—Selected measurements (mm) of certain fossil elements of *Ameiva exsul*.

	n	$\bar{x}$	Range
Dentary:			
Tooth row length	32	18.6	13.0–23.4
Articular + surangular:			
Width[1]	12	6.6	4.4– 9.1
Maxilla:			
Tooth row length	17	14.7	11.0–17.8
Frontal:			
Midsagittal length	4	12.5	11.3–13.5
Parietal:			
Greatest length[2]	5	10.0	8.2–12.0
Basale:			
Length[3]	8	9.5	8.5–11.7
Width[4]		15.2	10.4–19.6
Palatine:			
Length	2	9.4	8.3–10.4
Quadrate:			
Height	7	4.8	3.3– 6.5
Scapula:			
Length[5]	12	12.3	7.9–15.5
Sacrum:			
Width across diapophyses	14	10.5	9.0–12.0

[1] Measured from lateral lip of condylar surface to tip of angular process.
[2] Measured from frontal border to tip of supratemporal process.
[3] Measured from apex of angle formed by pterygoid processes to lip of occipital condyle.
[4] Measured across paraoccipital processes.
[5] Measured along anterior border.

259257); vertebrae (16 dorsal, 1 sacral, 1 caudal—USNM 259256).

San Miguel Cave: dentaries (1 left —USNM 259269); articular (1 right— USNM 259270).

Barahona IV: maxillae (1 partial left —USNM 259271); pelves (1 right— USNM 259272).

Description.—Dentary: 14 complete dentaries have tooth rows ranging in length from 6.6 to 10.8 ($\bar{x} = 9.1$). The average height is 3.0 at the position of the last tooth. Eighteen to 20 teeth or empty alveoli are present. The first two teeth are simple, terminating in conical crowns. Numbers four, five, and six are similar, but their crowns are more truncate. The crowns of the remaining teeth are more truncate still and slightly mesodistally compressed. Four or five mental foramina penetrate the labial face between the second and fourteenth teeth, but this surface is otherwise smooth and

convex over the length of the dentary. On larger specimens, the anterior end often is irregularly scored. The coronoid overlap is present posteriorly between the surangular and coronoid processes and extends forward to the penultimate tooth. Meckel's groove is open the length of the dentary, but nearly closed between the seventh and eleventh teeth. An intramandibular septum with a fused ventral border is visible posterior to the fourteenth tooth. A fossil dentary is shown in Fig. 21.

Articular + surangular: the largest of five bones from the post-coronoid portion of a mandible is 14.9 in total length and 2.6 wide anterior to the articular condyle. The quadrangular-shaped retroarticular process extends 3.7 beyond the posterior border of the condyle. The angular process is a vertically oriented knob on the medial side of the retroarticular process.

Maxilla: the most complete of five maxilla referred to this species is 9.1 from the premaxillary process back to the jugal process and 2.0 from the parapet of the jaw to the top of the nasal process (Fig. 21). This bone has fourteen teeth similar to those on the dentary. The four posterior teeth are the smallest and have the most truncated crowns. The teeth in the middle of the dental row are more chisel shaped. Five foramina penetrate the labial face in an irregular row between the third and ninth teeth. Three to five other foramina penetrate the anterior end of the nasal process and a single foramen is located high on the posterolabial side of the premaxillary process. Two scars occur on the medial edge of the alveolar border for articulation with the palatine and vomer.

Frontal: the unfused frontals of *Diploglossus pleei* are nearly square. The largest complete fossil specimen (Fig. 22) is 7.9 in mid-sagittal length and 7.3 across the parietal border. Fused osteoderms cover the bone dorsally except on the recessed nasal process. The suborbital processes are wide at their bases
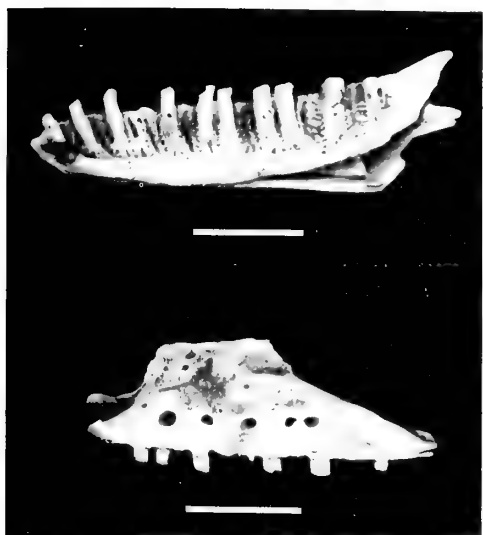
FIG. 21.—Fossil jaws of *Diploglossus pleei*. Lingual view of dentary (top, USNM 259258), labial view of maxilla (bottom, USNM 259261). Scale equals 3 mm.

and protrude medially as spoon-shaped flanges. Each frontal articulates anteriorly with the nasal and laterally with the prefrontal, posterolaterally with the postfrontal and posteriorly with the parietal. The pre- and postfrontals do not make contact laterally, although the prefrontal extends back over half the length of the frontal.

Parietal: two nearly complete parietals were recovered from Nesophontes Cave. The larger is 6.3 across its frontal border and 8.5 from the frontal border to the end of the supratemporal process. The ventral surface is concave for its anterior two-thirds, but rises thereafter to a rounded summit bearing the parietal fossa. Two lateral ridges converge toward the fossa from the frontal border.

Basale: a single basale and two separate otic elements are approximately of the same size and proportions. The basicranium consists of the otic capsules and occipital bones (Fig. 22). The basisphenoid is absent from the fossil. The distance between the sphenoccipital tubercles is 3.4.

Vertebrae: the vertebral centra of this lizard are smooth and flat and the

condyles are depressed and elliptical. Sacral vertebrae are fused at the zygapophyses as well as at the transverse processes distally. Fracture planes on autonomic caudal vertebrae pass in front of the transverse processes.

Comments.—The generic allocation of West Indian diploglossine lizards has fluctuated widely over the years. As many as four genera have been proposed —*Diploglossus*, *Celestus*, *Sauresia* and *Wetmorena* (Cochran, 1941; Grant, 1940; Schwartz, 1970), and as few as two— *Diploglossus* and *Wetmorena* (Under-

FIG. 22.—Fossils of *Diploglossus pleei*. Basale (top—occipital view, USNM 259265), frontals (bottom—dorsal view, USNM 259263). Scale equals 3 mm.

wood, 1959, Meszoely, 1970). Recently, four genera were again proposed by Strahm and Schwartz (1977), who resurrected *Celestus* and *Sauresia* in a compelling analysis of osteoderm structure. Retained in the genus *Diploglossus* are the species *anelpistus, delesarga, montisserati, pleei,* and *warreni.* Species assigned to *Celestus* are *barbouri, costatus, crusculus, curtissi, darlingtoni, duquesneyi, fowleri, hewardi, marcanoi, microblepharis, occiduus,* and *stenurus.* *Sauresia* includes two species, *sepsoides* and *agasepsoides* while *Wetmorena* remains monotypic *(W. hatiana).*

I have examined the skulls of most of these species and found little to distinguish them from one another except for size. The intramandibular septum is one of the more variable characters in that 1) the ventral border may be fused entirely, 2) fused anteriorly but not posteriorly or 3) free ventrally altogether. It is completely fused in *C. crusculus* and both species of *Sauresia;* free posteriorly in *W. hatiana, C. curtissi, C. darlingtoni, C. hewardi,* and *C. costatus* and completely free ventrally in *D. warreni, C. barbouri, C. stenurus,* and *D. pleei.* The fact that the intramandibular septum is completely free in recent skeletons of *D. pleei* and fused in the fossils is, at present, inexplicable. Moreover, the function of the structure is unknown. Perhaps it is associated with fossorial adaptations—i.e., fusion of the ventral border providing reinforcement to the jaw. I found no evidence that a free or fused ventral border was related to size or ontogeny. The fossils of *D. pleei* are the largest diploglossines in which I observed the fused condition. Estes (1964) discussed this structure in other anguinomorph lizards.

One dentary character distinguishing *D. pleei* from other West Indian diploglossines is the angular process at the back of the bone. In this species, the angular process extends backward well past the level of either the supra-angular process or coronoid process above it. The

angular process is parallel with the supra-angular process in *Sauresia, D. warreni* and *C. stenurus,* and shorter than the supra-angular process in *C. curtissi, C. darlingtoni, C. barbouri, C. hewardi, C. crusculus, C. hewardi,* and *W. hatiana.* It is absent from *C. costatus.*

The frontals of *D. pleei* are unusual in that they are nearly square instead of rectangular, a condition shared with *Wetmorena hatiana.* There is little medial constriction to the frontals of *D. pleei,* and the suborbital processes are shorter and more robust than in other species.

Much more study of West Indian and mainland diploglossine lizards will be necessary before their relationships are understood. For now, I have found no skull characters indicating four genera within the West Indian species. Certain characters are useful in distinguishing one species from another, but overall, the similarity in skull morphology bespeaks a close relationship amongst the group. Further analysis of osteology and integumentary structure is recommended.

Living *Diploglossus pleei* reach a snout-vent length of about 110. The fossil individuals had an average of 135 (98-160) based on dentary length and 135 (100-147) estimating from length of the maxillae.

Amphisbaenia

Amphisbaenidae

Amphisbaena sp. indet.

Material.—Blackbone 1: mandibles (1 partial left—USNM 259273); vertebrae (2—USNM 259274).

Description.—Two vertebrae and a nearly complete left mandible are similar to those of living *Amphisbaena.* The mandible (Fig. 23) is 4.5 as measured along its ventral border. The tooth row, bearing eight pleurodont teeth, is 3.1. The three anteromost teeth are pointed, recurved, and larger than those that follow. The five posterior teeth are equal in size except for the last which is

smaller. The teeth arise from a narrow dental shelf at an oblique, anteriorly directed angle and terminate as blunt cones. Overall, the mandible is high, linguilabially compressed and has a steep coronoid with a broken tip. Two foramina penetrate the labial side below tooth 4 and tooth 6. A single foramen is present anteriorly just lateral to the symphysis.

The two vertebrae have centra 2.1 and 2.3 long including the condyles. The neural arches are low, constricted in their middle and the pre- and postzygapophyses are broad and directed obliquely away from the midsagittal line. A rib tubercle is present on either side of the cotyle inferior to the prezygapophyses.

Comments.—Four of the ten species of *Amphisbaena* occurring in the West Indies are endemic to Puerto Rico, and a fifth, *A. fenestrata,* is restricted to the Virgin Islands. On Puerto Rico *A. schmidti* is known from the northwestern limestone region west of Dorado and *A. caeca* occurs throughout most of the island. Conceivably the fossils could represent either of these species. *Amphisbaena bakeri* is believed to be confined to the mountains between Mayagüez and Lares, but formerly its range may have

FIG. 23.—Fossil dentary of *Amphisbaena* sp. in lingual view (USNM 259273). Scale equals 2 mm.

included cave regions to the east. *Amphisbaena xera* is restricted to the arid southwest corner of the island. Apparently, the fossil individual was a subadult with an estimated snout-vent length of 130. As adults, the five species on the Puerto Rican Bank exceed 200 according to Thomas (1966), who reviewed the group. Other Antillean species are treated by Gans and Alexander (1962).

Serpentes

Typhlopidae

Typhlops sp. indet.

Material.—Blackbone 1: vertebrae (35 midbody, 1 caudal—USNM 259275-6).

Description.—Some of the snake vertebrae from Blackbone 1 are referred to *Typhlops* because of their small size, depressed neural arches, rudimentary neural spines, well-developed accessory processes, and knoblike synapophyses for rib articulation. An example is shown in Figure 24. List (1966) described the thoracolumbar vertebrae of typhlopid snakes, pointing out the flattened centra penetrated by one or two foramina on the ventral surface. The foramina may be laterally paired or single and median, but they usually are present in most species of *Typhlops*. The Puerto Rican blind snake, *Typhlops richardi,* is a species that List included among those bearing a single median foramen. This condition obtains in 28 of 35 fossil vertebrae. Most of the fossils are equal in size except for six which are one half as large. The largest vertebra has a centrum 2.4 in length including the condyle. The single caudal vertebra is distinguished by an enclosed hemal arch.

Comments.—Three species of *Typhlops* inhabit the island today, but only *T. richardi* occurs throughout the Puerto Rican Bank. *Typhlops rostellata* is widespread on Puerto Rico, but restricted to mesic situations. The third species, *T. granti,* is confined to the xeric southwest

part of the island. Although I made no osteological comparisons of these three, from List's (1966) generalizations I would not expect discernible differences in vertebral structure.

Schmidt (1928) gave a range of 210 to 310 total length for 14 individuals of *T. richardi*. Seventy-eight specimens of *T. rostellata* examined by Ruthven and Gaige (1935) varied in length from 104 to 227, while the maximum size they gave for *T. granti* is 154. There is probably a minimum of two individuals represented by fossils according to size, but this can not be said with much certainty. Most of the vertebrae came from an individual in excess of 300, which makes *T. richardi* a reasonable guess as to its identity.

Boidae

Epicrates inornatus Reinhardt

Material.—Guánica Bat Cave: dentaries (1 right—USNM 259278); maxillae (1 right—USNM 259279); palatine (1 left—USNM 259280); vertebrae (11 anterior, 17 anterior trunk, 24 midtrunk, 7 posterior trunk, 4 caudal—USNM 259281-2).

Cueva Clara: dentaries (1 right—KUVP 11524); maxillae (1 right—KUVP 11524); pterygoids (1 right—KUVP 11524); vertebrae (6 anterior, 17 anterior trunk, 8 midtrunk, 1 caudal—KUVP 11524).

Barahona IV: vertebrae (34 midtrunk—USNM 259285).

Barahona Dump No. 1: vertebrae (3 midtrunk—USNM 259286).

Blackbone 1: vertebrae (2 midtrunk—USNM 259277).

Nesophontes Cave: vertebrae (2 midtrunk—USNM 259283-4).

Above Horrible Bat Cave: vertebrae (1 midtrunk—USNM 259287).

Description.—The two dentaries, one each from Guánica Bat Cave (Fig. 25) and Cueva Clara are very similar to one another. Their tooth rows are 24.9 and 24.0 respectively. There are positions for 17 teeth, although neither specimen

has a full complement. The anterior three or four teeth are twice as large as those that follow, but all are sharply recurved. Posteriorly on the labial surface is a large, wedge-shaped emargination extending craniad to the level of the twelfth tooth. It is occupied in life by the surangular process of the compound

FIG. 24.—Fossil vertebrae in dorsal view of *Typhlops* sp. (top, USNM 259275); cf. *Alsophis portoricensis* (middle, USNM 259289); cf. *Arrhyton exiguum* (bottom, USNM 259296). Scale equals 2 mm.

bone. A single mental foramen penetrates the surface below the fourth and fifth teeth.

The maxilla from Guánica Bat Cave is the section posterior to the medial palatine process. The maxilla from Cueva Clara is nearly complete. This fossil, about two-thirds as large as the Guánica specimen, has a tooth row 23.3 long and positions for 19 teeth.

The single palatine bone is like that of modern *E. inornatus*. It has 6 teeth or empty alveoli and a thick, dorsomedially directed process forming a roof over the pterygoid notch at the back of the bone.

The expanded central portion of a left pterygoid is missing both ends of the bone, but it is otherwise unremarkable by comparison to the same structure in living *E. inornatus*. A row of small teeth and alveoli extends forward from the middle of the ventral surface at the level of the maxillary articulation.

Most of the fossils referred to this snake are vertebrae from various regions of the body. The generalized vertebra of *E. inornatus* has a neural arch that is emarginate in back and swollen above the zygantra. The zygapophyseal facets are oval and lie in a horizontal plane. The accessory processes are small and the condyles are round. There are approximately 230 presacral vertebrae in living individuals. The first 40 vertebrae are slightly broader than long and have thick, vertical neural spines and caudally directed hypopophyses. The hypopophyses on the next 20 vertebrae gradually diminish in size to form a midventral ridge along the centra. There are about 120 thoracic or midtrunk vertebrae that follow these. The midtrunk vertebrae increase in size and become much broader than long. The midventral hypopophyseal ridge widens, and the neural spine terminates in a flared rectangular cap (Fig. 25). The hypopophyseal ridge is narrow on the remaining presacral vertebrae, but the ridge expands into the base of the centrum cotyle.

These posterior trunk vertebrae are smaller than those at midbody and are approximately as long as wide. The caudal vertebrae have transverse processes that curve out and down. The paired hemal spines are short and directed backward.

Comments.—In their review of Hispaniolan *Epicrates*, Sheplan and Schwartz (1974) recognized two species in greater Puerto Rico—*E. inornatus* on Puerto Rico and *E. monensis* on Mona Island and the U.S. and British Virgin Islands. The authors stated (p. 100) that ". . . no other complex within Antillean *Epicrates* is more puzzling than
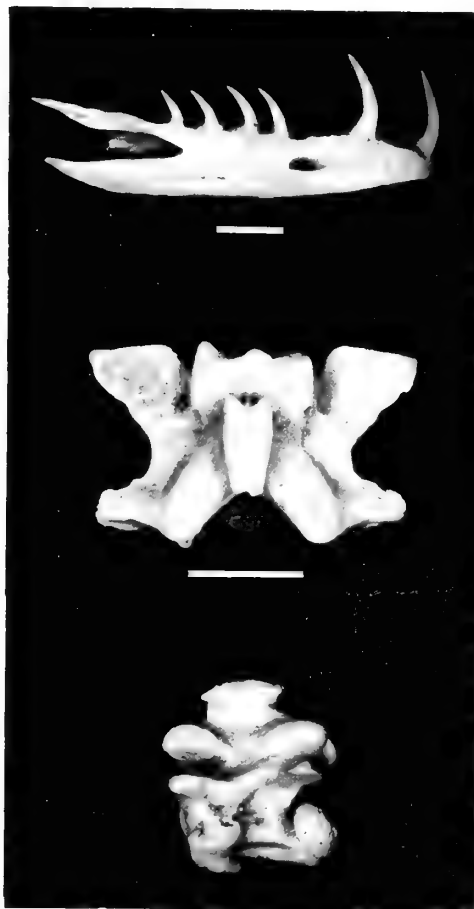

Fig. 25.—Fossils of *Epicrates inornatus*. Dentary (top, USNM 259278); trunk vertebra (middle—dorsal view, bottom—lateral view, USNM 259281). Scale equals 7 mm.

those taxa associated with Greater Puerto Rico." Part of the reason for this enigma is that the Mona Island subspecies, *E. m. monensis,* is known from very few specimens. It is most peculiar that the range of *E. inornatus* divides that of *E. monensis.* Sheplan and Schwartz accounted for this by proposing that at one time Puerto Rico was inhabited by two boas, a very large one, *E. inornatus,* and a small one *E. monensis,* that became extinct. If so, and the idea makes sense, the small one is not present in any of the fossil deposits. The fossils are from very large snakes. The smallest had an estimated snout-vent length of 1300, whereas the largest exceeded 1650. The maximum size known for *E. monensis* is 770, whereas *E. inornatus* may reach 1860 (Sheplan and Schwartz, 1974). The authors regarded *E. monensis* as quite distinct from either of the two small Hispaniolan species, *E. fordii* and *E. gracilis. Epicrates inornatus* is believed to resemble closely *E. subflavus* of Jamaica.

Little is known of the habits of *E. inornatus,* although it is widely distributed over the island, typically in wooded situations from sea level to 1050 meters at El Yunque. It may be associated with caves and talus slopes. *Epicrates angulifer* is partly cavernicolus. This species has been taken near cave entrances in Cuba and it is known to feed on bats. If these habits are applicable to *E. inornatus,* the fossil assemblage could be anticipated.

Colubridae

cf. *Alsophis portoricensis* Reinhardt and Lütken

Material.—Blackbone 1: vertebrae (10 trunk, 3 caudal—USNM 259288).

Barahona IV: vertebrae (12 trunk, 6 caudal—USNM 259294-5).

Nesophontes Cave: vertebrae (7 trunk, 1 caudal—USNM 259293).

Cueva Clara: vertebrae (4 trunk—KUVP 11524).

Blackbone 2: vertebrae (2 trunk—USNM 259289-90).

Rosaria River: vertebrae (2 trunk—USNM 259292).

Guánica Bat Cave: vertebrae (1 trunk—USNM 259291).

Description.—Vertebrae from seven caves are tentatively assigned to the Puerto Rican ground snake, *Alsophis portoricensis,* because of their similarity to this species. I have withheld definitive assignment because of the current systematic chaos among West Indian xenodentine snakes. However, the fossils can be distinguished from the only other Puerto Rican colubrid, *Arrhyton exiguum,* by several features (Fig. 24). The most obvious difference is size. On the average, *Alsophis portoricensis* is twice as large as *Arrhyton exiguum*—923 versus 438 maximum snout-vent length (Schwartz, 1966). The fossil vertebrae of *A. portoricensis* have an average centrum length of 5.9 and an interprezygapophyseal width of 4.7. The midbody vertebrae of *A. portoricensis* have elliptical zygapophyseal facets with accessory processes projecting anterolaterally. In *A. exiguum,* the zygapophyseal facets are circular and the accessory processes project laterally. The zygosphenal arch has a more undulating border in *A. exiguum* because the zygosphenes extend farther forward. The neural spines of *A. portoricensis* are high and narrow in comparison with those of *A. exiguum,* in which the spines are low and the neural arches themselves are depressed. The condyles of both species are round and oriented slightly dorsad. A midventral ridge is present on the centra of both species, but in *A. exiguum* the ridge is constricted anteriorly, forming a depression on either side of the ridge at the base of the cotyle.

The comparative differences in vertebral structure between these two snakes are subtle and intra-columnar variation tends to obscure their distinctions. In all, however, they are sufficient to differentiate the two species.

Comments.—The fossil vertebrae referred to *Alsophis portoricensis* probably

represent single individuals from each of the localities where they are found except at Blackbone 1 where three discrete sizes are present. Estimates of snout-vent length are based on measurements between pre- and postzygapophyses, across the accessory processes anteriorly, and midventrally from the edge of the cotylar lip to the end of the condyle. The smallest individual from Blackbone 1 had a snout-vent length of 325 to 350. The largest, from Cueva Clara, was 780 to 850, whereas the average snout-vent length of snakes from all caves was 700 to 725 (630-765).

The classification of West Indian colubrid snakes has never been stable and over the years the number of genera and species has continued to expand and contract. Dunn (1932) was first to make a serious attempt at working up a large segment of the group, mainly the Greater Antillean forms, and he relied heavily on a few superficial characters, for example sensory pits. More recently, Maglio (1970) addressed the problem using skull osteology. He compared all Antillean species and several mainland forms and proposed separate origins and derivations for the two Puerto Rican species. Maglio allied *A. exiguum* with the *funerus* species group of Jamaica. *Alsophis portoricensis* was placed in the *cantherigerus* group whose ancestral populations were to have island-hopped southeasterly from Cuba. Maglio's (1970) treatment of West Indian colubrids remains to be tested and current work on other neotropical zenodontine snakes suggests that major systematic revisions are still in order (Alan Savitzky, pers. comm.).

Alsophis portoricensis ranges throughout the Puerto Rican Bank in a multitude of habitats. Although it is rare or extinct on Vieques, St. Croix, Tortola, and St. Thomas, it persists on smaller cays and islets. The species is locally common on Puerto Rico, but in recent years no collector has been able to amass large series from any one locality and

apparently its restriction coincides with the introduction of the mongoose (Schwartz, 1966).

cf. *Arrhyton exiguum* Cope

Material.—Blackbone 1: vertebrae (20 trunk, 3 caudal—USNM 259296-7).

Nesophontes Cave: vertebrae (2 trunk—USNM 259298).

Description.—The general morphology of the vertebrae is discussed under the preceding description of *Alsophis portoricensis*. The vertebrae of *A. exiguum* are small; the largest fossil (Fig. 24) is 3.7 between pre- and postzygapophyses, the smallest 1.0. The anterior trunk vertebrae have caudally directed hypopophyses and the neural spines project beyond the posterior border of the neural arch. Their centra are shorter and narrower than the vertebrae posterior to them. The midbody vertebrae are elongate and lack hypopophyses, but retain a low hypopophyseal ridge. The neural arches are depressed. Caudal vertebrae have flat, anterolaterally directed transverse processes with broad bases that extend for over half the length of the centra.

Comments.—Fossils of *Arrhyton exiguum* from Blackbone 1 fall into three sizes—individuals with estimated snout-vent lengths of 115 to 125, 250 to 370, and 420 to 440. The individual(s) from Nesophontes Cave was (were) about 400. Schwartz (1967) gave maximum sizes for this species of 438 for females and 428 for males.

Arrhyton exiguum is a reclusive snake not frequently met in the field. Its range includes Puerto Rico, the Virgin Islands (with the possible exception of St. John), and many of the bank satellites. It is found most often in trash and rubble of fallen fronds and branches, and beneath logs and rocks from sea level to the El Yunque rain forest (Schwartz, 1967).

DISCUSSION

Comparison of the Cave Faunas.— Although the fossil herpetofaunas de-

scribed here are not necessarily a complete sampling of late Pleistocene species, their diversity is remarkable and deserves discussion. In all, 21 species represent 16 genera and 12 families. All modern genera of amphibians and reptiles indigenous to Puerto Rico are represented, with the exception of the geographically restricted gekko, *Phyllodactylus*. Two genera, *Cyclura* and *Leiocephalus*, no longer occur on the island. The 47 species of amphibians and reptiles living on Puerto Rico currently are grouped into 13 genera and 12 families. Six modern introductions are not included: *Hemidactylus brooki*, *H. mabouia*, *Bufo marinus*, *Hyla cinerea*, *Osteopilus septentrionalis* and *Rana catesbeiana* (Cochran, 1941; Trueb and Tyler, 1974; Schwartz and Thomas, 1975).

Some fossil localities have more species than others, and the number of individuals of any given species varies among them also. Relative abundance can be compared by determining the minimum number of individuals (MNI) of a species from each locality by counting the most abundant skeletal element from a particular side, either right or left. For example, the single most abundant skeletal element of *Ameiva exsul* from Blackbone 1 is the right dentary, of which there are 12. Thus, at least 12 individuals are represented as fossils. The results of this tabulation are recorded in Table 5.

Anolis cuvieri and *Ameiva exsul* are the most frequently occurring species as well as the most abundant individuals. Of the remaining 18 species, only 6 are present in four or more of the localities. These species are *Epicrates inornatus* (7), *Alsophis protoricensis* (7), *Anolis cristatellus* (6), *Peltophryne lemur* (6), *Leptodactylus albilabris* (5), and *Diploglossus pleei* (4). Evidently, the distribution and abundance of species as fossils is largely a consequence of prey vulnerability and the predatory habits of the owls, although the complexities of predator-prey ecology are such that the

most abundant prey species in an area may not necessarily be the most frequently represented in the diet of the predator. *Tyto cavatica* was obviously an efficient predator, and barn owls in general are opportunistic feeders (Craighead and Craighead, 1969), as demonstrated below.

The North American barn owl, *Tyto alba*, is common in the Greater Antilles, and its diet has been reported from the southern Bahamas, Hispaniola, and Grand Cayman Island and recently summarized by Morgan (1977). Morgan's comparisons of North American and West Indian barn owl roosts showed that, in general, the continental pellets were composed almost exclusively of mammals, whereas those from the West Indies, both fossil and Recent, contained birds, lizards, and frogs as well as small mammals. This is a result of the lower diversity and abundance of nonvolent mammals in the West Indies, both now and in the late Pleistocene. In both fossil and Recent barn owl deposits studied from the West Indies, birds are the most commonly occurring class of vertebrates and usually constitute a significant percentage of the total fauna. Bats are diverse in both fossil and Recent pellet remains from West Indian barn owl roosts, but they constitute a low percentage of the total number of individuals. Mammalian remains in modern West Indian owl pellets are dominated by *Rattus* and *Mus*, whereas the West Indian fossil deposits contain a much more diverse assemblage of all sorts of vertebrates. On Puerto Rico, the only mammal other than bats that was small enough to be taken by *Tyto cavatica* was the insectivore *Nesophontes*.

Reptiles and amphibians are extremely rare in North American barn owl deposits, but they occur in all known West Indian pellet remains in variable numbers. Fossil pellets tend to have a higher percentage of amphibian and reptile species than do modern ones. The newly collected birds and mammals from

TABLE 5.—Distribution and relative abundance (%) of species per fossil locality.

	Bb1		Neso		Bb2		BaIV		SnM		Guan		Per		Cla		All	
	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
Frogs																		
Leptodactylus albilabris	24	14.3	6	17.1	2	8.3			1	5.3							33	10.4
Eleutherodactylus spp.	45	26.8	1	2.9	1	4.2			1	5.3							47	14.9
Peltophryne lemur	21	12.5			12	50.0	1	9.0	3	15.8	2	20.0					39	12.3
Turtles																		
Chrysemys decussata									1	5.3							1	0.3
Lizards																		
Sphaerodactylus sp.	2	1.2															2	0.6
Anolis cuvieri	3	1.8	12	34.3	2	8.3	3	27.0	3	15.8	2	20.0	12	42.9	7	58.3	52	16.5
A. cristatellus	5	3.0	2	5.7	2	8.3	1	9.0	3	15.8			2	7.1			15	4.7
Anolis spp.	32	19.1															32	10.1
Cyclura pinguis	2	1.2	1	2.9	2	8.3	1	9.0	2	10.5			1	3.6	1	8.3	10	3.8
Leiocephalus etheridgei	7	4.2											6	21.4			13	4.2
L. partitus											1	10.0	1	3.6			2	0.6
Mabuya mabouya	4	2.4															4	2.4
Ameiva exsul	12	7.4	2	5.7	2	8.3	2	18.0	4	21.1	2	20.0	6	21.4	2	16.7	33	10.4
Diploglossus pleei	1	0.6	8	22.9			1	9.0	1	5.3							11	3.5
Amphisbaenids																		
Amphisbaena sp.	1	0.6															1	0.3
Snakes																		
Typhlops sp.	2	1.2															2	0.6
Epicrates inornatus	1	0.6	1	2.9			1	9.0			2	20.0			1	8.3	6	1.9
Alsophis portoricensis	3	1.8	1	2.9	1	4.2	1	9.0			1	10.0			1	8.3	9	1.9
Arrhyton exiguum	3	1.8	1	2.9													4	1.3
Total	168		35		24		11		19		10		28		12		316	

[1]Abbreviations: MNI—minimum number of individuals; Bb1—Blackbone 1; Neso—Nesophontes Cave; Bb2—Blackbone 2; BaIV—Barahona IV; SnM—San Miguel Cave; Guan—Guánica Bat Cave; Per—Cueva del Perro; Cla—Cueva Clara; All—all fossil localities including those not tabulated. See text.

the Puerto Rican caves have not been described yet, and thus, the relative proportion of the amphibians and reptiles is unknown. Bird remains are plentiful, however, and more plentiful in Blackbone 1 than in the other localities (Storrs Olson, pers. comm.). Both fossil and modern deposits are similar in that the herpetofauna often is dominated by one or two species. For example, on Cayman Brac *Anolis sagrei* accounted for nearly 47% of a fossil fauna, but seven other lizard species were present, and on neighboring Grand Cayman Island *Anolis conspersus* constituted almost 65% of a recent deposit (Morgan, 1977). On Barbuda in the Lesser Antilles, three species of *Anolis* composed 85% of the lizard remains from one cave in which seven lizard species were present (Etheridge, 1964a). The Puerto Rican faunas follow this same pattern. *Eleutherodactylus* dominates the highly diverse Blackbone 1 fauna, and as noted previously, only 8 amphibian and reptile species out of 21 occur in 4 or more of 14 localities. Overall, *Anolis cuvieri* and *Ameiva exsul* account for over 26% of all individuals. These two lizards are approximately equal in size (125-150 SVL) and apparently were optimum prey. They differ in habits. *A. cuvieri* is a forest-canopy dweller, whereas *A. exsul* is active on the ground in open habitat. Both are diurnal species, and *Tyto cavatica* may have hunted for them in the early evening when *A. exsul* was still moving about, but when *A. cuvieri* had stretched out for the night on an exposed perch.

Cyclura pinguis and *Epicrates inornatus* are among the more frequent species in the cave remains on Puerto Rico, but they are represented by few individuals and constitute a low percentage of the total fauna in any cave. Their presence as fossils is probably not a result of predation, however, as adults of *Cyclura* exceed 7,000 gm body weight (Carey, 1975), whereas the average *Tyto alba* weighs about 300 gm (Craighead and Craighead, 1969). It is impossible

that *Tyto cavatica*, which was slightly smaller than *T. alba*, preyed on lizards of this size. However, juveniles may have fallen prey as indicated by an individual with a snout-vent length of 150 in Blackbone 1. Juveniles would be exposed to late afternoon predation, for *Cyclura pinguis* reappears at this time when ambient temperatures drop below 30°C (Carey, 1975). I have no data on body weights of *Epicrates inornatus*, but adults are too large to have been preyed on by *T. cavatica*.

The total species diversity and abundance of individuals from all localities reflects an obvious bias from Blackbone 1 (Table 5). For example, frogs account for 53.6% of the Blackbone 1 fauna and 37.6% for all localities combined. However, frogs account for no more than 20% of the total fauna from any other cave except Blackbone 2. Moreover, *Eleutherodactylus* spp. alone constitutes nearly 27% of the Blackbone 1 herpetofauna, but the genus is represented by only one individual in each of two other deposits. The absence of *Eleutherodactylus* and other small species (*Sphaerodactylus*, *Typhlops*, small anoles) from most of the caves is probably the result of sampling bias. The fossil matrix from Blackbone 1 was screened and picked to a finer degree because of the large quantity of bones and obvious antiquity of the deposit. I did similar screening of a smaller sample of fossil matrix from Nesophontes Cave, but was unable to recover any fossils that added to the faunal list for that cave. The richness of the Blackbone 1 fauna, whether a consequence of sampling bias or not, affects the sum total of diversity and relative abundance in two ways. First, the Blackbone 1 fauna greatly increases the total diversity of species. Secondly, it alters the total relative abundance of a species in its favor, as for example *Eleutherodactylus*. Thus, Blackbone 1 is exemplary of the potential diversity and abundance of specimens in fossil owl pellet deposits; the cave contains many species

that have a low probability of turning up as fossils on account of small size or secretive habits.

Some of the small, secretive species might not have been prey of the barn owl, but of the smaller Puerto Rican screech owl, *Otus nudipes,* or to an extinct burrowing owl, *Speotyto* sp., remains of both of which are common in the Blackbone 1 deposits (Storrs Olson, pers. comm.). These owls also appear to have been preyed on extensively by the barn owl. Although Wetmore (1922) suggested that the screech owl may have been responsible for the remains of small birds in other Puerto Rican caves, both this species and the forms of *Speotyto* are largely insectivorous. Some of the small, secretive reptiles could have been ingested secondarily by the avian predators. *Sphaerodactylus, Amphisbaena* or *Typhlops* may have been eaten by another reptile, which, in turn, was consumed shortly thereafter by an owl. *Alsophis portoricensis* is known to be partly ophiophagus (Schwartz, 1967) and may have preyed on *Amphisbaena* or *Typhlops.*

It is more difficult to compare the faunas chronologically in the absence of stratigraphic control, there being no certain means of establishing the relative ages of the cave faunas nor the duration of deposition in each case. Most deposits probably overlap chronologically and thus are partly contemporaneous. The fossil material from Blackbone 1 may be older than the other cave remains because of its discoloration and partial permineralization. An approximate date of 20,000 y.b.p. is assigned cautiously to the Blackbone 1 fossils and correlates with climatological evidence discussed in the next section. San Miguel, Nesophontes, Blackbone 2 and Barahona IV Caves have similar species composition and differ mainly in the relative abundance of particular species. The color and texture of the fossils from these caves is similar and there are no obvious morphological differences in the bones

that would suggest chronological trends. Intraspecific variation is no greater between caves than within them, with respect to tooth count, dermal sculpturing, size, or other morphological features of the fossils. Cueva del Perro may be close in age to Blackbone 1 because it is the only other locality in which the extinct lizard *Leiocephalus etheridgei* occurs. The absence of this lizard from the other deposits suggests that the animal may have become extinct prior to use of the caves by owls. On the other hand, Cueva del Perro also shares the extinct species *Leiocephalus partitus* only with Guánica Bat Cave, the fauna of which is rather recent in appearance (color of fossils) and composition. Cueva del Perro and Blackbone 1 probably represent faunas of some antiquity, and caves that remained active as accumulation sites for a long time.

Fossils of several species exhibit some structural differences distinguishing them from their living relatives. For example, gigantism occurred within *Leptodactylus albilabris, Peltophryne lemur, Anolis cuvieri,* and perhaps *Diploglossus pleei;* each achieved snout-vent lengths in excess of any individuals of their species known today. The reasons for this are unclear, but it has also been reported in fossils of other Antillean lizards, such as *Aristelliger lar, Anolis ricordi, Anolis sagrei,* and *Anolis bimaculatus* (Etheridge, 1964a, 1965). Curiously, among modern West Indian amphibians and reptiles only the "giant anoles" (*A. cuvieri, A. roosevelti, A. equestris, A. ricordi*), *Diploglossus anelpistus,* and *D. warreni* still attain unusually large size. Other morphological differences between fossil and Recent species include the dentary sculpturing on male *Anolis cristatellus,* the fused intramandibular septum in *Diploglossus pleei,* and the condition of Meckel's groove in the two new species of *Leiocephalus.* In each instance, all fossils, regardless of locality, differ from all modern specimens.

The Paleoenvironment.—It is reason-

able to assume that the owls living in Puerto Rican caves hunted near their roosts rather than in distant areas of the island. Their prey, therefore, was obtained in the immediate vicinity, which permits an estimate of the probable habitat of the area based on ecological requirements of the prey species. Although there is a dearth of knowledge on habits and life histories of most West Indian amphibians and reptiles, the diversity of fossil species from the caves of the Ciales region exceeds any previously described paleoherpetofauna in the Antilles and invites interpretation in light of current ideas on late Pleistocene climatology.

Pleistocene glacial climatic fluctuations have been given increased attention in recent years by geologists and biologists. Current theory favors numerous glacial advances and retreats during the last half million years. However, the latitudinal climatic gradient produced by glaciations has yet to be determined, and only the fact of severe world-wide climatic fluctuations is established. Data on fluctuations in paleotemperatures and comcomitant changes in humidity have been augmented by palynological studies on both continents in the New World. It is of particular interest that equatorial as well as temperate regions were affected by Pleistocene climatic fluctuations.

In the West Indies, core samples taken from the central Caribbean Sea have yielded an undisturbed record of late Pleistocene O^{18}/O^{16} isotopes that show fluctuations in sea water temperature indicative of climatic change (Emiliani, 1966; Emiliani and Rona, 1969). Temperature correlations covering the last 450,000 years show 17 major fluctuations from about 22° to 28°C. Approximately 65,000 years ago the last full interglacial ended and sea water began cooling until a low of 22°C was reached around 15,000 to 20,000 years ago. Thereafter, a warming trend began which continues to the present. Emiliani's data

were corroborated by Bonatti and Gartner (1973) from an analysis of $CaCO_3$-free sections of the core showing fluctuations in concentration ratios of kaolinite to quartz. Kaolinite is a layered silicate commonly produced by chemical weathering during humid climatic conditions. The kaolinite to quartz ratio is highest during the warmer interglacials and lowest during glacial maxima when compared with Emiliani's isotopic temperature curve. Thus, lower temperatures also indicate periods of aridity because cooler sea surface temperatures would reduce the supply of water vapor to the atmosphere.

Haffer (1974) discussed evidence that, on land, Pleistocene glaciation in northern South America produced alternations in humid and dry climatic periods in the tropics that resulted in shrinkage and expansion of lowland forests in eastern Colombia and interior Guyana. Indeed, Pleistocene pulsations apparently had a profound influence on structuring the modern Amazonian forest biota (Simpson and Haffer, 1978; Haffer, 1979). Immediately north of the Greater Antilles in Florida, pollen studies strongly indicate dry climates in a period from about 37,000 to 13,000 years ago. Core samples taken from midpeninsular lake sediments are dominated by pollen characteristic of a savanna of dune scrub and scattered stands of oak during that period (Watts, 1975; Moran, 1975).

Let us relate this to the Antilles. Lowland thorn-scrub characterizes the West Indies, dominating areas with less than four inches (10 cm) of rain per month (Howard, 1973). Periodic flooding coupled with poor drainage due to serpentine and siliceous soils, alternates with desiccation to produce retarded tree growth, and hence, savannas. Savannas and thorn-scrub occur on many islands of low relief and also in rain shadows on mountainous islands such as Puerto Rico (Figs. 2 and 3). The cool, arid regime 65,000 to 15,000 years ago probably favored a more extensive xeric flora on

Puerto Rico, as it did in northern South America and Florida. Today, savannas occur on the northwest coast of Puerto Rico only at the cape region near Isabella, but during the late Pleistocene they probably were more widespread. It is difficult to say just how far savannas or a dry coastal flora reached into the more interior regions of the island, or to what elevations. The cave area around Barahona is 180 m above sea level and is characterized today by a mixture of secondary, deciduous species with seasonal flowering. The prevalence of fossils of xerophilic amphibians and reptiles supports a hypothesis that savannas or a dry coastal flora extended to this region 10,000-20,000 years ago. *Cyclura* and *Ameiva,* for example, are heliophilic, essentially open country lizards that are common as fossils from the Ciales region. *Cyclura* is now extinct there. *Ameiva exsul* is uncommon, being now practically restricted to coastal regions with mostly xeric habitat. The high incidence of *Anolis cuvieri* as a fossil from the cave regions appears to contradict the argument because of the strictly arboreal habits of this lizard. However, a closed savanna adjacent to the more open areas could account for its occurrence. Moreover, the lizard simply may have inhabited lower elevations to compensate for cooler montane temperatures. *Anolis cuvieri* is not now restricted to upland localities *per se,* but it requires dense tree foliage and most of the habitat is presently at higher elevations.

Few other of the commonly occurring fossil species are directly helpful in determining the paleoenvironment. For example, *Peltophryne lemur* is known today from widely scattered localities on the island, and most of these are at elevations no higher than the Barahona Valley. The toad apparently has an affinity for more xerophytic habitats, but this has not been confirmed. *Leptodactylus albilabris* occurs over the island in regions of suitable moisture for egg laying, but it is a terrestrial species and

its presence as a fossil is not unexpected. *Diploglossus pleei* also is fairly abundant as a fossil. It is a shade-loving species and a denizen of forest floors and leaf litter. Today the lizard is found principally in mesic situations in the interior upland, although I have collected it in the coastal lowlands north of Ciales near Manatí. *Diploglossus pleei* apparently adapts to disturbed environments, for it is found in the coffee plantations on the mid-altitude slopes. *Leiocephalus* is not especially abundant as a fossil, but two extinct species are present. Most *Leiocephalus* are xerophiles, but some, such as the Hispaniolan *L. melanochloris,* are shade and forest dwellers (Schwartz, 1965). Thus, it is difficult to relate the Puerto Rican *Leiocephalus* to a late Pleistocene xeric habitat, but I am inclined to favor an arid regime for them.

After evaluating the composition of the fossil herpetofauna, one is left with the impression that the late Pleistocene environment in the vicinity of the cave region may have been in a transitional zone between xeric, open habitat towards the coast and a more closed, mesic situation extending to the interior. Unfortunately, neither the flora nor the amphibians and reptiles presently occupying the Barahona Valley can be used to test this hypothesis conclusively. For example, *Anolis cristatellus, Anolis pulchellus,* and *Eleutherodactylus coqui* are the most common species in the Ciales region today, but they are equally common at low and middle altitudes in disturbed and undisturbed habitat throughout the island. In other words, these species are not useful ecological indicators because of their vagility and the same is assumed for the Pleistocene. (For further discussion of this point see Rand and Williams, 1969.) Species such as *Ameiva exsul* and *Cyclura pinguis* are most helpful in interpreting the past environment because of their more specialized ecological requirements.

Interpretation of past environments should account for any extinctions of the

animals that occupied them. The three species in the fossil assemblages that became extinct presumably were xerophilic—*Leiocephalus etheridgei, L. partitus* and *Cyclura pinguis*. Their demise may have coincided with a return to humid conditions in the past 13,000 years. *Cyclura pinguis* could have persisted into Subrecent times on Puerto Rico because its remains on St. Thomas are associated with kitchen middens (Miller, 1918). Increasing humidity with concomitant expansion of forest in the Barahona Valley probably eliminated *Ameiva exsul* from most of this area and restricted populations to coastal areas. Interestingly, southwestern Puerto Rico in the vicinity of Guánica Bat Cave boasts habitat seemingly suitable for the arid forms that became extinct on the other side of the island. Of the three, only *L. partitus* occurs as a fossil from the Guánica locality. The absence of *Leiocephalus etheridgei* and *Cyclura pinguis* from the Guánica deposits is enigmatic because the occurrence of *L. partitus* suggests that the habitats were reasonably similar on either side of the island. Of course, the absence of fossils does not prove that the lizards were not in the vicinity.

The assumption that climatic changes that took place in the past 13,000 years were responsible for the extinction of the three lizards does not explain how the animals survived the previous interglacials occurring over the last 450,000 years. Indeed, this requires that the species were present and subject to the rigors of changing environments with potentially similar effects. Extinctions of other vertebrates in the West Indies were not uncommon in the late Pleistocene and sub-Recent times and a general explanation is desirable. A number of bird species (many of them xerophyllic forms) disappeared along with small mammals (Olson, 1978). This is in contrast to the North American continental fossil record for the same period, where extinctions mostly involved the mammalian mega-

fauna and associated vultures. The majority of the amphibians and reptiles known as fossils from the late Pliocene and Pleistocene are still with us today (Gehlbach, 1965). Further data on the North American fossil record of amphibians and reptiles are being reported rapidly (Holman, 1976 and other works), and misidentification of previously described fossils is not uncommon, which could mitigate this argument in either direction. One explanation for the greater survival of the North American herpetofauna during the Pleistocene is that continental species have broader distributions containing multiple habitats and thus are more likely to survive local extinctions. Insular species with fewer and smaller populations (i.e., absolute size) are not as fortunate. Further documentation and dating of West Indian fossils is essential if this problem is to be resolved.

Zoogeographic Considerations.—The comparative recency of the fossil herpetofaunas from Puerto Rico and other West Indian islands precludes much insight into their history. The fossils are essentially modern, usually referable to extant species and genera, and provide little information for extending historical biogeography into the Tertiary. The fossil evidence does demonstrate, though, that the modern herpetofauna of Puerto Rico was well-established in the late Pleistocene. Since then the distribution of amphibians and reptiles has been subject to changing environments, by both natural occurrence and human interference, and to fragmentation of the Puerto Rican Bank by eustatic rising in sea level.

Little is known of pre-Pleistocene sea levels, but an estimate of 120 m has been given for maximum Pleistocene lowering (Donn et al., 1962). By 14,000 years ago sea levels were 75 m below the present level, though Puerto Rico and all of the Virgin islands except St. Croix were still a single land mass. Sea level rose to 15 m below present level after 8,000 years ago, submerging small islands off the
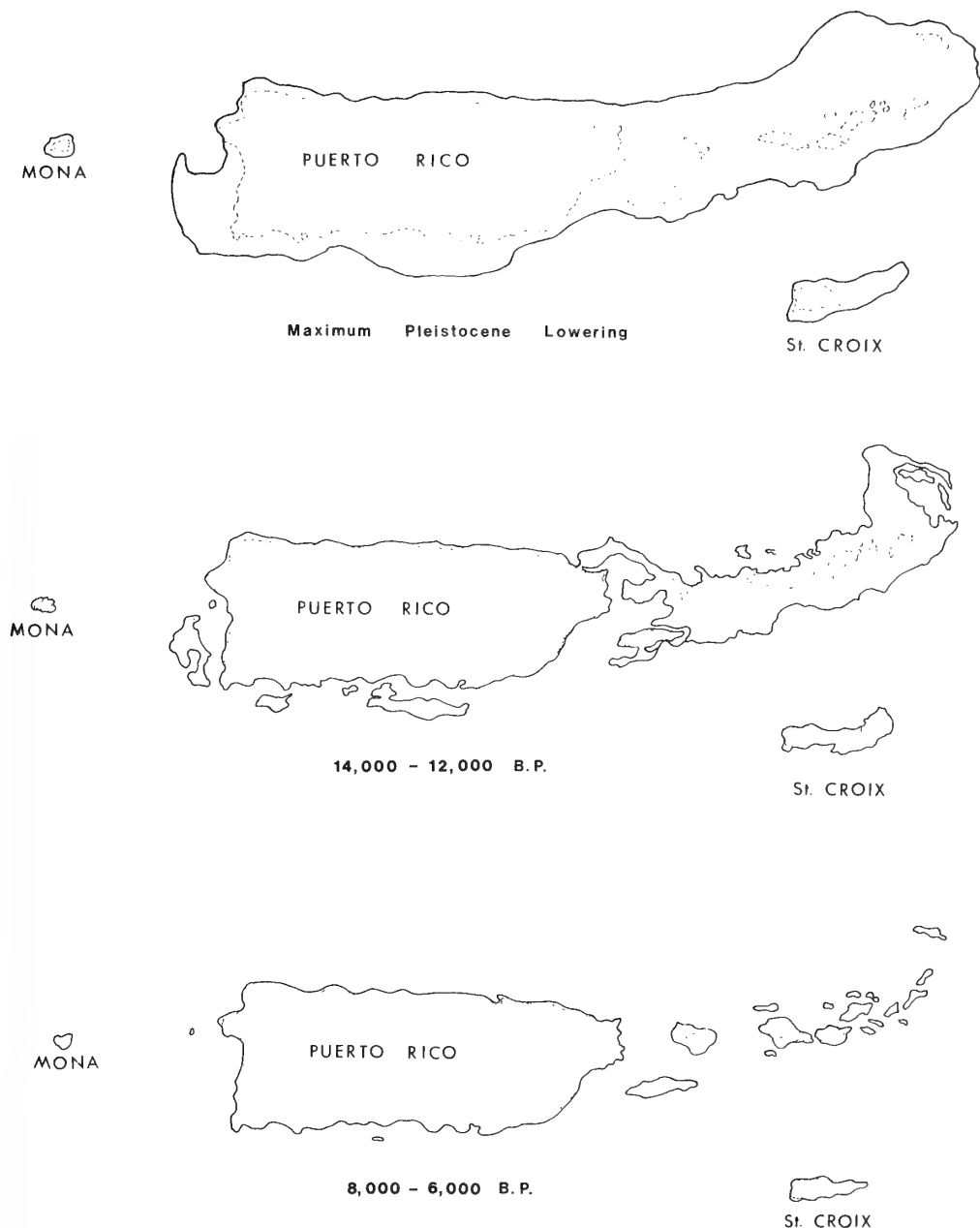
FIG. 26.—Fragmentation of the Puerto Rican Bank by eustatic rising in Pleistocene sea levels. The islands were united as a single land mass during maximum Pleistocene lowering as shown at top. Sea levels were about 75 m below present level in the middle diagram and fragmentation was essentially complete when sea levels rose to about 15 m below present level in Holocene time (bottom). The islands as they exist today are shown by the dashed lines. (Data taken from Heatwole and MacKenzie, 1967.)

eastern shelf and separating all the Virgin Islands from Puerto Rico and one from another (Fig. 26). The configurations of the islands were roughly the same as today because of the steepness of the slopes, but their areas were larger, especially that of Anegada. For the past 6,000 years sea levels have fluctuated slightly above or below present level (Heatwole and MacKenzie, 1967).

Because the islands of the Puerto Rican Bank were not separated until 8,000 years ago, it is not surprising that none of the smaller islands has more than two endemic species (less than 10% of their herpetofauna). On the other hand, Mona Island and St. Croix have a high number of endemics (50% and 66%, respectively) because these islands have been separated from Puerto Rico for a long time, if, in fact, they were ever connected (Heatwole and MacKenzie, 1967). Puerto Rico also has a larger number of endemic species (60%), but the island is much larger than any of the others on the bank and the habitats are much more diverse. Those species that persist on the Virgin Islands do so in an environment of low relief and rainfall comparable to their habitat on Puerto Rico, now and during the late Pleistocene. Predictably, they include *Eleutherodactylus cochranae*, *E. antillensis*, *Ameiva exsul*, *Anolis cristatellus*, the grass/bush anoles *A. pulchellus* and *A. stratulus*, *Sphaerodactylus macrolepis*, *Typhlops richardi*, and both species of colubrid snakes. *Cyclura pinguis* persists as a relict on but one island, Anegada. It is unlikely that the more mesic-adapted species such as *Diploglossus pleei*, the rain forest anoles like *A. occultus*, *A. krugi*, and most of the *Eleutherodactylus* were ever well established on these "islands" in the Pleistocene.

Some amphibians and reptiles have disappeared from the bank islands in modern times, for example, *Anolis roosevelti*, the giant anole known only by a few specimens from Culebra Island off the east coast of Puerto Rico, has not been seen since 1932 (Schwartz and Thomas, 1975). *Anolis roosevelti* was absent from all of the fossil deposits on Puerto Rico and during the late Pleistocene was probably excluded from the west end of the bank by *A. cuvieri*. Whether or not either of these lizards was ever present on any of the other bank islands is unknown. *Peltophryne lemur* is another example of a species whose range has been constricted. The toad was last collected on Virgin Gorda in 1931 and now may be extinct on that island.

Insights into earlier events in Puerto Rico's zoogeographic history are seen in the island's geographically central position in the West Indian archipelago. The Puerto Rican herpetofauna is strikingly Greater Antillean, in spite of the fact that the island is no closer geographically to the northern islands than to the Lesser Antilles to the south. For example, nearly all Puerto Rican *Eleutherodactylus* are members of the *auriculatus* group whose other Antillean members are found mostly on Hispaniola and Cuba (Schwartz, 1969). Over one hundred species of *Eleutherodactylus* occur in the Greater Antilles compared with five in the Lesser Antilles. *Peltophryne lemur* is a southern representative of the Cuban-Hispaniolan complex of endemic bufonids, which does not reach the Lesser Antilles. West Indian *Chrysemys* are restricted to the Greater Antilles except for introductions on Guadelope. The *macrolepis* complex of Puerto Rican *Sphaerodactylus* probably resulted from a single invasion from the north by the *notatus* group (Schwartz, 1978). Puerto Rican *Anolis* represent a radiation of the Alpha Section that originally invaded Hispaniola and subsequently dispersed and differentiated as two groups—the *cristatellus* and *bimaculatus* series. Interestingly, Williams (1976) accounted for the entire diversification of West Indian *Anolis* by assuming only three mainland invasions. *Cyclura* and *Leiocephalus* are also Greater Antillean genera.

Most likely, *Ameiva exsul* is allied with *A. chrysolaema* on Hispaniola rather than with any northern Lesser Antillean species, such as *A. pleei* (Baskin and Williams, 1966). *Diploglossus pleei* probably is a derivative from an ancestral species resembling *D. warreni* on Hispaniola. The West Indian anguid lizard fauna is exclusively Greater Antillean, except for *Diploglossus montiserrati* on Montserrat Island. *Amphisbaena* is the only genus with its greatest Antillean diversity on Puerto Rico; five species occur in the Puerto Rican Bank, Hispaniola has four, and Cuba has one. The genus is absent from the Lesser Antilles. *Epicrates* also is restricted to the Greater Antilles. The systematics of West Indian xenodontine snakes is not resolved, but the majority of species are Greater Antillean.

There are two Puerto Rican genera whose affinities may be in the Lesser Antilles. *Leptodactylus* reaches the Greater Antilles only as far as the southeast corner of Hispaniola. *Phyllodactylus* has been collected in Hispaniola, but otherwise it is restricted to the Puerto Rican Bank *(P. wirshingi)* and Barbados *(P. pulcher).* Another lizard, *Mabuya mabouya,* is an Old World derivative now widespread in the Neotropics (a number of species may be masquerading as *Mabuya mabouya*) including the West Indies. Only one other species of skink, *M. lineolata,* occurs in the islands (Hispaniola).

Clearly, the Puerto Rican herpetofauna is an assemblage of taxa on the periphery of a Greater Antillean radiation, and most of Puerto Rico's species were derived from Hispaniola. The great diversity of amphibians and reptiles on Hispaniola (173 species) and the island's proximity to Puerto Rico has overshadowed chance invasion through the Lesser Antilles. In addition, the distribution of several fossil and living species indicates that the Greater Antillean herpetofauna extended farther south in "sub-Recent" times. There are fossils of *Leiocephalus,*

Eleutherodactylus, and possibly *Cyclura* on Barbuda (Etheridge, 1964a; Auffenberg, 1959; Lynch, 1966), and modern representatives of *Diploglossus* on Montserrat and *Leiocephalus* on Martinique. Further documentation of this pattern must await additional paleontological work in the Lesser Antilles.

The antiquity of the Greater Antillean herpetofauna is also demonstrated by paleontological investigations of the North American Tertiary. *Leiocephalus* is known from the early Miocene of Florida (Estes, 1963) and the middle Miocene of Nebraska (Carl Wellstead, pers. comm.), and a diploglossine lizard was found recently in early Eocene deposits of Wyoming (Jacques Gauthier, pers. comm.). These finds are important because the probability now exists for a North American origin of at least some of the Antillean lizards heretofore assumed to be South or Central American derivatives. Wherever the source, understanding the origins of the Antillean herpetofauna will require knowledge of fragmentation events as well as dispersal. Given the possibility of arid regimes predominating at periodic intervals throughout the Pleistocene, any modern biogeographic analysis must now take into account the possibility of a multitude of restructured and relictual distributions throughout the last half million years alone, which substantially increases the zoogeographic complexity. Continued investigation of the Antillean fossil record is our best tool for understanding the zoogeographic consequences of Pleistocene climates.

SUMMARY AND CONCLUSIONS

The known fossil record of West Indian amphibians and reptiles is no older than late Pleistocene, and the few existing studies deal almost exclusively with lizards from the Greater Antilles. This study analyzes the first fossil herpetofaunas known from Puerto Rico, and the

most extensive yet reported from the West Indies. Thousands of fossil bones of amphibians and reptiles were collected from 14 caves on the island; one cave in particular, Blackbone 1, produced a unique abundance of species of lizards, frogs, and snakes. In the total fossil fauna are 21 species representing 16 genera and 12 families, many of which are improbable finds for cave deposits. The predatory role of the owl, *Tyto cavatica*, that deposited the fossil pellets biased the sample by favoring animals of certain size and habits. The material from Blackbone 1 includes fossorial species, for example typhlopid snakes and an amphisbaenid, as well as other small, secretive species such as leaf-litter gekkos *(Sphaerodactylus)* and canopy-dwelling anoles. Secondary ingestion may account for some of these, reflecting, in part, the trophic structure of the community. Apparently *Tyto cavatica* was an efficient and opportunistic hunter. Also among the remains are two previously unknown species of the iguanid lizard genus *Leiocephalus,* and fossils of the previously enigmatic rock iguana *Cyclura portoricensis* (Barbour), which is placed in the synonymy of *C. pinguis* living today on Anegada Island.

The species composition of the fossil faunas indicates that the environment of the cave region was a xeric, savanna-like habitat quite in contrast to the mesic conditions that prevail there now. Corroborative evidence from deep-sea drilling projects in the Caribbean show that arid and cool climates were present in the West Indies 15,000-20,000 years ago, the approximate time of fossil deposition. An environmental shift to more mesic conditions subsequent to 13,000 years ago restructured the herpetofaunal community and may have brought about the extinctions of *Leiocephalus* and *Cyclura* on the island and restricted the xerophiles to coastal habitat.

The herpetofauna of Puerto Rico is Greater Antillean in its affinities and derived largely from Hispaniola. As a whole, the amphibians and reptiles of the Greater Antilles are relictual forms, and the Puerto Rican taxa are now at the periphery of a Greater Antillean distribution that extended well into the Lesser Antilles during the Pleistocene.

Future paleontological work is strongly recommended for the West Indies. In cave faunas, particular attention should be directed towards potential stratigraphic sequences of species and continued efforts at confident dating of the material. Pre-Quaternary fossils and sediments should be sought in an effort to extend our knowledge of West Indian vertebrates further into the past.

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APPENDIX I: Comparative Material Examined. (Museum acronyms are given on page 3.)

Frogs

Peltophryne empusa, AMNH 61409; *P. fluviatica,* AMNH 87235; *P. gundlachi,* AMNH 99764; *P. guntheri,* AMNH 54743; *P. lemur,* RT 4075; USNM 27148, 27150; *P. longinasa,* AMNH 101835; *P. peltocephala,* USNM 28021, 029484, 90888, 167528; *Eleutherodactylus antillensis,* KU 124244; *E. cooki,* MCZ 18653; *E. coqui,* MCZ 43221; KU 79950; GKP 261, 305; *E. karlschmidti,* FSM 24200; MCZ 18711; *E. locustus,* KU 124249; *E. portoricensis,* GKP 042, 254; MCZ 85212; *E. richmondi,* MCZ 18922; *E. wightmanae,* KU 124255; *Leptodactylus albilabris,* GKP 302; MCZ 87339; *L. wagneri,* KU 125940.

Lizards

Amphisbaena fenestrata, KU 87856; *Anolis cooki,* GKP 0301; *A. cristatellus,* KU 49022-9, 49035, 49043-4; *A. cuvieri,* MCZ 57898-9, 10960, 35967-71, R127119 (alcohol); *A. evermanni,* MCZ 132041; *A. equestris,* KU 61391; USNM 167530; *A. gundlachi,* GKP 0154; KU 79198; MCZ 131917; *A. krugi,* FSM 39764-5; MCZ 132087; *A. occultus,* MCZ 146683; *A. pulchellus,* GKP 0290; FSM 29766-7; MCZ 36073; *A. ricordi,* USNM 72632; *A. stratulus,* GKP 0303; KU 49053-57; *Ameiva c. chrysolaema,* REE 1459; *A. exsul,* KU 045557; MCZ 131904; *A. f. festiva,* KU 117468; *A. lineolata,* REE 1482; *A. taeniura,* REE 1456; *A. undulata*

parva, KU 117473; *A. wetmorei,* MCZ 36437; *Basiliscus vittatus,* USNM 71430; *Celestus barbouri,* ASFS 16081; *C. costatus,* FSM 12308-1; *C. curtissi,* ASFS V42502; *C. crusculus,* FSM 20935, 21743; *C. darlingtoni,* ASFS V45037; *C. hewardi,* ASFS V11534; *Conolophis pallidus,* REE 1382, 1447; *C. subcristatus,* USNM 165756; *Ctenosaura quinquecarinata,* USNM 30564; *C.* sp., USNM no data; *Cyclura carinata,* FSM 30206-8, 30407, 30425, 32674, 32676, 33291, 33293-4, 33265, 35122, 37024, 39770-1; USNM 88819; *C. cornuta,* FSM 33651, 34750; REE 383, 1967; *C. cychlura,* FSM 19066; *C. figginsi,* KU 174796; *C. mattea,* USNM 59358-9; *C. macleayi,* REE 228; FSM 21910; *C. pinguis,* ASFS V21995; *C. portoricensis,* MCZ 1008-13; *Diploglossus pleei,* GKP 0268-70; MCZ 131510; *D. warreni,* ASFS V42502; *Dipsosaurus dorsalis,* USNM 29182; *Enyalioides praestabilis,* USNM 7796; *Enyaliosaurus clarki,* USNM 21452; *Laemanctus serratus,* USNM 82178; *Leiocephalus apertosulcus,* MCZ 3404; *L. barahonensis,* REE 1821; *L. carinatus,* FSM 14373, 18929, 23082, 21739, 21907, 39763; REE 1469, 1816, 1805-6, 1808; USNM 81709; *L. cubensis,* MCZ 7281a; *L. cuneus,* FSM 8226, 8263-71, 8444, 8468-70; *L. greenwayi,* REE 1814; *L. inaguae,* ASFS 10330, 10337, 10346; FSM 11525; *L. loxogrammus,* MCZ 38136; *L. lunatus,* REE 1815; *L. macropus,* REE 1819; USNM 59167; *L. melanochloris,* REE 1802; *L. personatus,* REE 1803, 1811; *L. pratensis,* ASFS V9844, V9851; *L. psammodrommus,* FSM 33737-8, 34804-6, 25124-6; *L. punctatus,* ASFS V8732, V8736, V8747; *L. raviceps,* MCZ 11376; *L. schreibersi,* REE 1810; FSM 12273, 12276; *L. stictogaster,* REE 1810; *L. vinculum,* REE 1812; *Liolaemus chilensis,* KU 161700; *L. fitzingeri,* USNM 36933; *L. kingi,* USNM 36918; *L. lineomaculatus,* USNM 36896; *L. multiformis,* KU 133796; *L. nigriceps,* USNM 1642516; *L. nitidus,* KU 161770; *L. tenuis,* USNM 5518; *L. weigmanni,* USNM 70477; *Mabuya mabouya* KU 113519; *Morunasaurus annu-*

laris, USNM 204240; *Ophryoessoides iridescens,* USNM 200912; *Plica plica,* AMNH 61314; *P. umbra,* USNM 204266; *Phrynosoma cornutum,* USNM uncat., *Sauresia agasepsoides,* ASFS V40784; *S. sepsoides,* ASFS V40855; *Sceloporus cyanogenys,* USNM 47715; *S. undulatus,* USNM 739, 29194; *Sphaerodactylus macrolepis,* KU 49001-4; GKP 299; *Stenocercus varius,* USNM 201321; *Tropidurus albemartensis,* AMNH 77624; *T. torquatus,* USNM 148772; *Uracentron flaviceps,* USNM 201390; *Uranoscodon superciliosa,* USNM 202682; AMNH 61304; *Urosaurus ornatus,* USNM 16055; *Wetmorena haitiana,* FSM 12314; ASFS V20917.

Snakes

Alsophis portoricensis, RT 4829; KU 045669; *Arrhyton exiguum,* GKP 0274; MCZ 5430; *Epicrates cenchris,* GKP 110; *E. inornatus,* FSM 14434; MCZ 4684; *Typhlops richardi,* GKP 0275.

APPENDIX II: PREVIOUSLY RECORDED FOSSIL OCCURRENCES OF AMPHIBIANS AND
REPTILES IN THE WEST INDIES (EXCLUSIVE OF ARCHAEOLOGICAL STUDIES). ALL ARE
LATE PLEISTOCENE TO SUB-RECENT. (* = Extinct species.)

Barbados

Testudinidae
    (?) *Geochelone* sp.*   Ray (1964)
    Iguana iguana   "

Barbuda

Leptodactylidae
    *Eleutherodactylus barbudensis**   Auffenberg (1959), Lynch (1966)
    (= *Hyla barbudensis* Auffenberg)
Gekkonidae
    Thecodactylus rapicauda   Auffenberg (1959), Etheridge (1964a)
Iguanidae
    Anolis bimaculatus leachii   Etheridge (1964a)
    Anolis sp. (medium)   "
    Anolis sp. (small)   "
    *Leiocephalus cuneus**   "
    Genus and species indet.   "
       (cf. *Cyclura, Conolophis*)
Teiidae
    Ameiva griswoldi   Auffenberg (1959)
Colubridae
    Pseudoboa (cf. *P. cloelia*)   "

Cayman Islands

Leptodactylidae
    Eleutherodactylus planirostris   Morgan (1977)
Hylidae
    Osteopilus septentrionalis   "
Gekkonidae
    Aristelliger praesignis   "
Iguanidae
    Anolis conspersus   "
    Anolis sagrei   "
    Cyclura nubila   "
    Leiocephalus carinatus   "
Anguidae
    Celestus crusculus   "
Typhlopidae
    Typhlops biminiensis   "
    Typhlops caymanensis   "
Boidae
    Tropidophis caymanensis   "
Colubridae
    Alsophis cantherigerus   "
Crocodylidae
    Crocodylus cf. *acutus*   "

Cuba

Hylidae
  Osteopilus septentrionalis   Koopman and Ruibal (1955)
Testudinidae
  Geochelone cubensis*   Williams (1950), Auffenberg (1974)
Gekkonidae
  Tarentola americana   Koopman and Ruibal (1955)
Iguanidae
  Anolis lucius   ″
  Anolis equestris   ″
  Leiocephalus sp.   ″
Colubridae
  Alsophis cantherigerus   ″

Curaçao

Testudinidae
  Geochelone sp.*   Hooijer (1963)

Dominican Republic

Gekkonidae
  Aristelliger lar   Etheridge (1965)
Iguanidae
  Anolis chlorocyanus   ″
  Anolis cybotes   ″
  Anolis ricordi   ″
  Leiocephalus apertosulcus*   ″
  Leiocephalus personatus   ″
Teiidae
  Ameiva chrysolaema   ″
  Ameiva taeniura   ″
Anguidae
  Celestus costatus   ″
  Celestus stenurus   ″

Jamaica

Gekkonidae
  Aristelliger lar (= *A. titan*)   Hecht (1951)
  Aristelliger praesignis   ″
Iguanidae
  Leiocephalus jamaicensis*   Etheridge (1966a)

Mona Island

Testudinidae
  Geochelone monensis*   Williams (1952), Auffenberg (1974)

Navassa

Testudinidae
  Geochelone sp.*   Auffenberg (1967, 1974)

New Providence

Gekkonidae
    Tarentola americana   Etheridge (1966c)
Iguanidae
    Anolis carolinensis   ″
    Anolis distichus   ″
    Anolis sagrei   ″
    Cyclura sp.   ″
    Leiocephalus carinatus   ″
Teiidae
    Ameiva auberi   ″
Testudinidae
    Geochelone sp.*   Auffenberg (1967)

Puerto Rico

Iguanidae
    Cyclura pinguis (= *C. portoricensis*)   Barbour (1919)

St. Thomas

Iguanidae
    Cyclura pinguis (= *C. mattea*)   Miller (1918)

Sombrero Island

Testudinidae
    *Geochelone sombrerensis**   Auffenberg (1967, 1974)

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53. Evolutionary relationships, osteology, and zoogeography of leptodactyloid frogs. By John D. Lynch. Pp. 1-238, 131 figures in text. June 30, 1971. Paper bound.

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69. The *Eleutherodactylus* of the Amazonian slopes of the Ecuadorian Andes (Anura: Leptodactylidae). By John D. Lynch and William E. Duellman. Pp. 1-86, 8 figures in text. August 29, 1980. Paper bound.

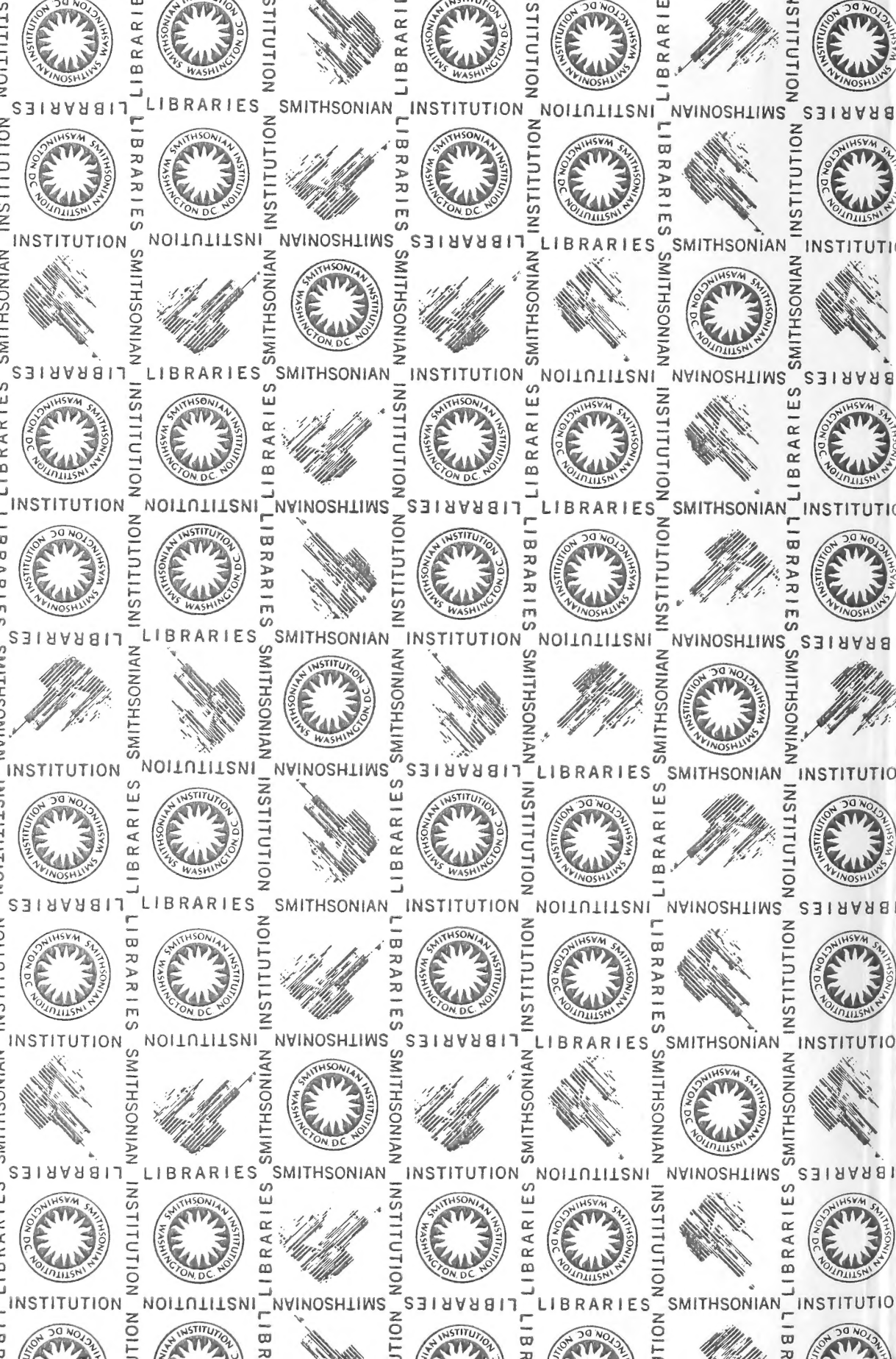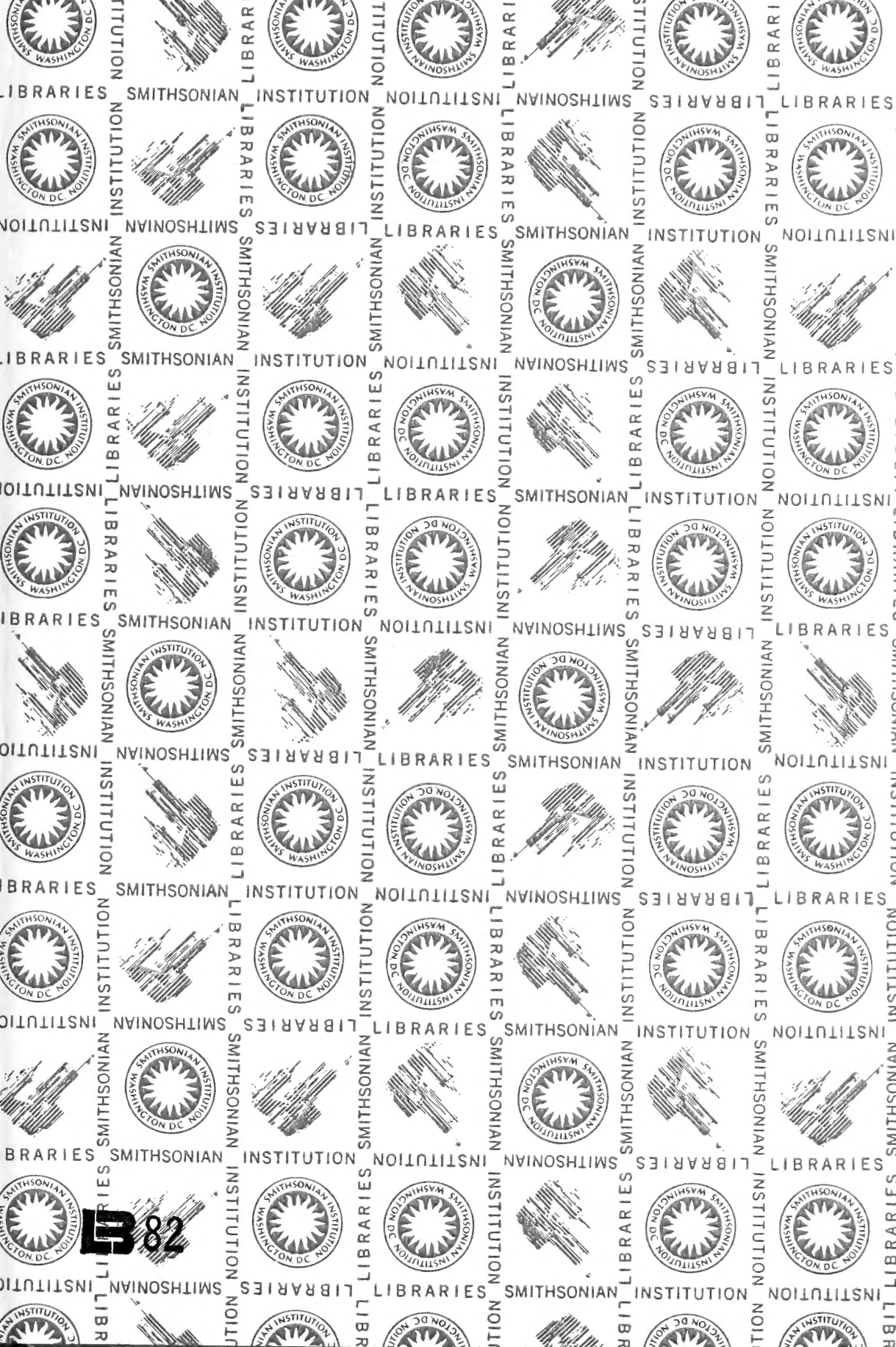70. Sexual size differences in reptiles. By Henry S. Fitch. Pp. 1-72, 9 figures in text. February 27, 1981. Paper bound.